S101 Units 20 and 21

THE OPEN UNIVERSITY

Science : A Foundation Course

20 Diversity and Evolution

21 Communities of Organisms

The Open University
Science: A Foundation Course

Unit 21
Communities of organisms

Prepared by the Science Foundation Course Team

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SCIENCE

Acknowledgements

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Figures

Figures 10 and 18 courtesy of G. C. Varley; *Figures 11, 13 and 17* from H. N. Southern (1970) 'The natural control of a population of tawny owls' in *Journal of Zoology*, Vol. 162, The Zoological Society of London; *Figures 19–21* from G.C. Varley *et al.* (2nd edn) (1973) *Insect Population Ecology*, Blackwell Scientific Publications.

Filmstrips

Frames 8–10 courtesy of G. C. Varley; *Frames 11–14* Nature Conservancy Council.

Contents

Table A List of terms and concepts used in Unit 21

Assumed from general knowledge	Introduced in a previous Unit	Unit No.	Introduced or developed in this Unit	Page No.	Developed in a later Unit	Unit No.
agricultural practices (some general idea only)	conservation of energy and different forms of energy	8	agricultural production and energy input	21	biochemical aspects of respiration	24
climates over the world (general idea only)	combustion involving uptake of oxygen and release of carbon dioxide	15	anthropogenic changes	47	carbon cycle	32
examples of plants from continents other than Europe	DDT and other insecticides	16/17	arrested and deflected climaxes	47	combustion of fossil fuels	32
feeding habits of common British animals	definition of species	18, 20	assimilation*	11	human food supply	32
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	fecundity	18	biological control of pests*	42		
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	pheromones as insecticides	16/17	carnivores*	10		
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	some sorts of plants and animals	20	climax community*	47		
	use of logarithms	14/15, *HED*†	common and rare species	29		
	vital activities of living organisms, especially nutrition, respiration	18	community*	8		
			consumers*	10		
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			decomposition	22		
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			density dependent mortality*	37		
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			diatoms	15		
			ecosystem*	8		
			energy balance	11		
			environment	7		
			equilibrium species*	47		
			fecundity*	26		
			fertilizers	23		
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			heterotrophes*	10		
			human birth rates and death rates	51		
			insecticides	43		
			integrated control of pests*	44		
			K (generation pre-reproductive mortality)*	30		
			k-values*	29		

* You should be able to define and explain the use of these terms (see Objective 1 on p. 55).

† The Open University (1979) S101 HED *The Handling of Experimental Data*, The Open University Press.

Table A (*continued*)

Assumed from general knowledge	Introduced in a previous Unit	Unit No.	Introduced or developed in this Unit	Page No.	Developed in a later Unit	Unit No.
			key factor mortality*	36		
			life tables	28		
			litter	15		
			mineralization	22		
			mortality	26		
			myxomatosis	48		
			net primary production*	11		
			niches*	24		
			nitrogen cycle*	22		
			nitrogen fixation	23		
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			physico–chemical factors*	7		
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			photosynthesis	10		
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			primary producers*	10		
			production*	10, 14		
			production and biomass	17		
			regulating mortality factors*	36		
			reproduction	25		
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Study Guide for Unit 21

This week's work concerns the biological discipline called 'ecology' (from the Greek for 'house' and 'study'); it deals with the interactions of organisms of the same and different species and of organisms and their environments. These interactions are important to human beings because ecological principles apply to human food supplies and human environments.

Your study of *Communities of organisms* includes:

1 Reading the main text of Unit 21.

2 Watching TV 21, 'Rabbits and chalk grasslands'.

3 Listening to Radio 11, 'Fisheries and food'.

4 Carrying out the Home Experiment for Unit 21, '*Drosophila* survey'.

5 Answering the appropriate parts of CMA 48 and TMA 06.

You should have started the *Drosophila* experiment while you were studying Unit 18, and you may not finish it until you reach Unit 24, but it is an ecological experiment so you should think about the principles involved as you work through the text of Unit 21.

During this week, you should start the Home Experiment related to Unit 22; that is, you should plant out your peas so that they are ready to 'harvest' next week. Consult the instructions for Home Experiment 22 before you proceed with your study of Unit 21.

You will need your calculator for Sections 2 and 3. It is essential that you are familiar with how to obtain and manipulate logarithms; refer back to Unit 14 and to *HED* if you have misgivings about your understanding of logarithms. The actual calculations in Unit 21 are very simple, and you will find the ecological principles clearer if you carry out the calculations for yourself. **HED**

The Filmstrips related to this Unit are Filmstrips 21.1 to 21.4. A full list is given at the end of the Unit. Filmstrip 21.1 contains illustrations of animals and plants mentioned in the text; you may find it an advantage to have them handy.

You will need your viewer and Filmstrip 21.2 beside you while you study Section 4.1; you are asked to examine four of the Frames as you work through the text. Filmstrips 21.3 and 21.4 illustrate TV 21 (see the *Broadcast Notes*) but they are also relevant to Section 4.1.

You will find it helpful if you have read through Sections 4 and 4.1 before you view TV 21. If necessary, you can read these two Sections before studying Sections 2 and 3. It is advisable to read the Introduction and Section 1 first, because they set the scene for the rest of the Unit. Sections 2, 3 and 4 are each complete in themselves and relatively independent of the others, so they could be studied in any order.

The Radio programme on fisheries is transmitted in the week following that in which we expect you to study Unit 21. You should have read Sections 2, 3 and 5 before you listen to it.

The Audio-vision component of this week's work is associated with the Home Experiment, '*Drosophila* Survey'; you should have used it when you started the experiment. You may wish to refer to it several times to help you with the identification of the species of *Drosophila* and the parasitic wasps.

Introduction to Unit 21

All living organisms are adapted to the environments in which they normally live; if this were not true, then the theory of natural selection could not possibly be justified. You studied in Units 18 and 20 some types of adaptation that appear to contribute to the survival of those species that show them. In this Unit, you will study a range of common environments and their components, to which the species living in them must be adapted. The types of environmental factors that affect populations of organisms are defined in Section 1. The three following Sections discuss three different approaches to ecology and the final main Section, Section 5, very briefly draws your attention to some effects of human populations on communities of other organisms.

Ecologists have moved from a purely descriptive 'natural history' approach to two main lines of quantitative research. The first is the study of the structure of communities in terms of the throughput of energy and chemical compounds; this is called *production ecology*; its principles are discussed in Section 2. The quantitative study of food interrelationships demonstrates that there are principles that explain why the mass of organisms that can live in particular environments is limited; these principles are relevant to human food production. Another approach to studying community structure is based on the cycling of certain chemical elements that are essential components of living organisms. Work steadily through Section 2, making sure that you understand the examples; but do not try to remember the details of the interrelationships in the River Thames and in Wytham (pronounced wy-tam) Wood.

The second quantitative approach is the study of numbers of organisms of different species and how these numbers vary in time and space. Section 3 is concerned with the reasons for changes in numbers of individuals in a population both during the life span of a generation and over longer periods. Some populations fluctuate wildly in numbers and others remain almost stable over many years—why? Some organisms are always rare and others are always common—why? These are the two main questions asked in the study of *population dynamics*, and the answers are important in the management of natural resources and especially in devising systems of pest control. Again, try to understand the examples, and therefore the principles involved, and do not try to remember details.

Section 4 is a fairly short descriptive Section concerned with long-term changes in the identity and number of species in communities (i.e. in their composition). The impact of rabbits on the communities in which they live became clear as a result of the 'natural experiment' of myxomatosis; the theme of rabbits as ecological factors is also covered by TV 21.

In the final Section, we consider the effects of human populations on their environments: there are short discussions of human population changes and of some of the ecological problems of providing sufficient human food. Radio 11, on fisheries, is related to this Section.

This Unit contains many references to species of plants and animals; these are given their scientific names when first mentioned but are generally referred to by their common names (if any). If there were no named examples, the text would be vague and unsatisfactory; however, the examples are chosen to illustrate general principles and it is these that are important.

The reason for giving the scientific names is to make the references as precise as possible; common names often vary from place to place. *You are not expected to remember the scientific names* but, in some cases, if you understand their derivation, they tell you about features of the organisms. The practice of using scientific names is commended to all aspiring ecologists because they are used internationally; their exact pronunciation does not matter and indeed varies from country to country.

1 Environments, ecosystems and communities

environment

For each individual organism, its *environment* is a given place at a given time, and can be defined by:

physico–chemical factors

1 Its position on the Earth, which largely determines a series of environmental features that are called *physico–chemical factors* and include: the nature of the living space (whether it is sea or land, soil or water); the chemical constituents of the living space and its physical properties; the climate.

biotic factors

2 The assortment of other organisms present, which together make up the *biotic factors* of the environment. Biotic factors may alter physico–chemical factors locally, for instance by changing the 'microclimate' or chemical constituents; their main impact is usually through the provision of or competition for food, living space and shelter.

If it is to survive, an organism must be able to cope with all the problems presented to it by the physico–chemical and biotic factors of the place in which it lives. To study these problems fully, it is necessary to consider the anatomy, physiology and life history of all the organisms present, as well as the local geology and climate. This Unit is limited to a few examples of the types of problem investigated by ecologists.

From your general knowledge, you will know that different species have different distributions in the world, for example polar bears live in the Arctic and penguins mostly live in the Antarctic or South Temperate areas. A biologist who is sufficiently well informed can sometimes say very precisely whence came a given sample of organisms, collected 'in the wild', and what the physico–chemical conditions were at that place. For example, if the mammals collected included a koala bear, they must have come from Australia and from a part of that continent where

certain species of *Eucalyptus* trees grow; koala bears have a very narrow distribution and eat a few species of *Eucalyptus* only and no other food. Many other species have very limited distributions, for example, the coelacanth fish *Latimeria chalumnae*, which lives in the Indian Ocean just north of Madagascar, off the Comoro Islands (and was recognized as a living example of coelacanths only in 1939 when a specimen came to the attention of a fish expert in South Africa). One of the parasites that students very occasionally collect in the Open University *Drosophila* Survey had not been recognized until it was collected in Oxford in 1970. The name *Tanycarpa punctata* was given to it in 1976 (see Filmstrip 18.4, Frame 27). Its known distribution in 1977 was: near and in Oxford; near Ellesmere Port in Cheshire; and two villages a few miles north of Portsmouth. A systematic search might reveal more localities, but it is clear that this species is much rarer than the other two *Drosophila* parasites that students collect and breed. In contrast, there are a number of species that are very widely distributed, for example, bracken (a fern, *Pteridium aquilinum*; Filmstrip 21.1, Frame 1), the common reed *Phragmites communis* (Filmstrip 21.1, Frames 2 and 3), the starling *Sturnus vulgaris* and the house mouse *Mus musculus*. The last two have spread round the world with Europeans but the two plants have spread independently of human activities. The present distribution of any species is the result of its history since its first appearance and depends on where it originated and its subsequent dispersal from that area; its potential distribution will depend on how tolerant it is of environmental conditions and what sort of dispersal mechanism it has.

Filmstrip 18.4

Filmstrip 21.1

As with most sciences, the early development of ecology was as a descriptive science, based on the compilation of lists of organisms present or absent from various places. When species are listed for different areas, it is apparent that they form non-random associations which are called *communities*. These consist of populations of several or many different species (plants, animals and micro-organisms) found together in a definite area. Each community exists in a non-living environment with its local climate; the community and its environment make up an *ecosystem*. Communities and ecosystems can be studied at different levels—for instance, the community of an oak-wood (Filmstrip 21.1, Frames 4 and 5) includes a large number of smaller communities such as those of the oak-trees, of the hazel shrubs, of the 'herbs' (this term describes non-woody flowering plants such as bluebells) under the trees, of the 'litter' of fallen leaves and so on.

community

ecosystem
Filmstrip 21.1

So an ecosystem consists of:

a community of organisms	*plus*	its environment

An oak-wood community includes:	An oak-wood environment includes:
plants, for example trees (oaks), shrubs (hazel) and herbs (bluebells, grasses); animals, for example earthworms, insects (caterpillars), birds (tawny owls, tits) mammals (deer, voles, foxes); and micro-organisms, for example some fungi and soil bacteria.	physico-chemical factors, for example climate, soil; *plus* biotic factors, for example interactions with other members of the community that provide or compete for food and shelter or are predators.

The oak-wood ecosystem itself is part of a larger terrestrial ecosystem, probably a lowland area of Britain, which in turn is part of the island ecosystem of Great Britain. Even this island ecosystem is not a unit independent of all others: birds and butterflies and other less conspicuous organisms, as well as people, can move in and out from neighbouring continental areas. So it is necessary to define ecosystems and communities carefully when discussing and comparing them.

There is considerable public interest in and awareness of the effects of human activities on the environment and on other species of organisms. Any hope of predicting the results of increased or changed pressures on the environment must depend on understanding how ecosystems function and the underlying structure of communities of organisms. All agricultural practices interfere with natural ecosystems and involve the maintenance of artificial, usually simplified, communities; to cope with weeds and insect pests economically requires understanding of the interactions of individuals of different species—as competitors for environmental resources or as predators and prey. Thus the study of ecology is not only basic to understanding how natural selection operates but also of great importance in food production and in the maintenance and improvement of human environments.

1.1 Objectives of Section 1

Now that you have completed this Section, you should be able to:

(a) Explain how biologists use the following terms: physico–chemical factors and biotic factors; community; ecosystem.

(b) Suggest or assess hypotheses explaining the observed distribution of species of organisms in terms of their tolerance of physico–chemical factors and their past history.

To test your understanding of this Section, try the following SAQs.

Answers to SAQs begin on p. 56.

SAQ 1 (*Objective* (*a*)) Mark the following statements as either TRUE or FALSE.

(a) A community consists of many organisms all of the same species.

(b) The distribution of plants all over the world is greatly affected by climate, an important physico–chemical factor.

(c) Within climatic belts, the distribution of plants is not affected at all by the physico-chemical factors of soil type and altitude.

(d) The distribution of animals can sometimes be explained in terms of the biotic factor of food supply.

(e) Ecosystems are theoretically self-contained units consisting of an environment plus a community of organisms; such an ideal condition is seldom observed in nature.

SAQ 2 (*Objective* (*b*)) Brown trout *Salmo trutta* live and breed in rivers in Europe, North Africa and north-western Asia where the summer water temperature normally does not exceed 20 °C. They are also found in similar rivers in New Zealand. In the tropics, they are found in streams in East Africa (Kenya and Uganda) above about 2 000 m altitude, and they live in South Africa (Natal) above 1 500 m altitude. Rank the hypotheses (i)–(iv) according to how plausible they seem as explanations for these observations on the distribution of brown trout.

Hypothesis (*i*) Brown trout once had a world-wide distribution but are now restricted to areas where river water temperatures are within certain limits because the physiology of the fish has changed and they can no longer tolerate high water temperatures.

Hypothesis (*ii*) Brown trout once had a world-wide distribution but are now restricted because the tropics have become much warmer and the fish are limited by their physiology to living where water temperatures do not rise above about 20 °C.

Hypothesis (*iii*) Brown trout are native either to Europe or to New Zealand, probably to the former; they have been introduced into other parts of the world, where conditions seem suitable, to provide angling.

Hypothesis (*iv*) Brown trout are native to Europe (because they are widely distributed there); they are found in various other places, where the climate is suitable, because their eggs stick to the feet of ducks and geese which fly great distances, occasionally carrying eggs that survive the journey if released into a suitable river.

2 Ecosystems and production ecology

Study comment In Sections 2.1–2.3, the way in which communities are linked together by their energy requirements is discussed. We consider in turn: the sources of energy for individual organisms; the contrasting energy sources of plants, animals and micro-organisms; the grouping of organisms according to their types of food and the linking of species by patterns of energy flow. The pattern of energy flow is analysed for a simple aquatic ecosystem and a more complicated terrestrial ecosystem. The concept of 'trophic level' is explained and used in the analysis of how ecosystems function.

One obvious way in which organisms of different species interact is that some animals eat other animals or plants. The process of *nutrition* is a 'vital activity', as you read in Unit 18; all living organisms need some source of energy because other vital activities, such as growth and reproduction and responsiveness, require expenditure of energy. Nutrition is the process by which energy is acquired by an organism.

nutrition

> From what substances do *you* acquire energy? By what internal physiological process is energy made available for you to read this text?

You acquire energy from your food. Probably you eat a mixed diet that includes bread, meat, eggs, cheese and vegetables and you drink a variety of beverages including milk. These substances are digested in your gut (stomach and intestine), and products of digestion are absorbed into your body through your intestine and stored in your liver and in fat deposits. As you read this text, your body is 'using' energy through the process of *respiration* in which glucose (a sugar, derived from the digestion of your food) is combusted with oxygen (breathed into your lungs) and thus energy is made available to your muscles, nerves, sense organs and brain. You will read about biochemical aspects of respiration in Unit 24. Here, it is sufficient for you to realize that respiration can be represented by:

respiration

$$\text{sugar} + \text{oxygen} \rightarrow \text{carbon dioxide} + \text{water} + \text{energy}$$

The bulk of the food you eat is derived from other organisms, both plants (e.g. wheat and potatoes) and animals (milk, cheese, eggs, meat), so you are a *consumer* obtaining your energy from other organisms.

consumers

Some of the chemical energy in your food is transformed into kinetic energy (movement) or gravitational potential energy (when you stand up); but eventually, it is all transformed into thermal energy, that is, it is dissipated as heat. You will be aware of the heat when you take energetic exercise but it is also produced in all your other activities. In all animals, but especially when they are growing, some of the food is converted into new living material; this increase in amount of body material (biosynthesis) is called *production.*

production

> Are all living organisms consumers? If not, suggest how those that are not consumers acquire energy.
>
> All *animals* are consumers; that is they are dependent for their energy on other organisms. But most green plants are not consumers; recall from Unit 18 that they make use of some of the energy in sunlight in the process called photosynthesis.

2.1 Autotrophes and heterotrophes

Photosynthesis is characteristic of green plants; these are able to combine water and carbon dioxide to synthesize sugars, releasing oxygen at the same time. The energy for this synthesis comes from sunlight and is made available through the green pigment chlorophyll. Because plants can make sugars from the simple compounds, water and carbon dioxide, they are called *primary producers.* Plants grow by producing new body material but they require extra substances for growth. Plants absorb inorganic salts (nitrates, phosphates and sulphates) from their environments and thus acquire nitrogen, phosphorus and sulphur (and some other elements), which are essential for the synthesis of proteins and other materials necessary for growth. Because they can synthesize their sugars and proteins entirely from inorganic substances—carbon dioxide, water, mineral (inorganic) salts—if provided with light of appropriate wavelengths, plants are sometimes called *autotrophes* (from the Greek for 'self' and 'food').

photosynthesis

primary producers

autotrophes

Organisms that cannot use light energy to synthesize sugars and proteins from inorganic substances but must digest 'food' manufactured by other organisms are called *heterotrophes* (from the Greek for 'other' and 'food'). Animals are heterotrophes and so are some plants such as fungi (mushrooms and moulds). If animals eat plants, as cows do, they are called *herbivores* (from the Latin for 'grass' and 'devour'); if, like lions, they eat other animals, they are called *carnivores* (from the Latin for 'flesh' and 'devour'). Animals, such as earthworms, that feed on fragments of dead and decaying plant and animal material are called *detritivores*

heterotrophes

herbivores

carnivores

detritivores

(from the Latin for 'wearing away' and 'devour'). Fungi that grow on decaying plant and animal material are called *saprophytes* (from the Greek for 'putrid' and 'plant'). *Parasites* are organisms (animals, fungi and even plants) that are wholly dependent on a host organism (of another species) for their food.

saprophytes
parasites

Once organisms have made sugars or obtained them by digesting food, the majority, both plants and animals, depend for the release of energy on the process of *respiration* in which glucose is combusted with oxygen. Commonly, the oxygen is absorbed from the environment, and this uptake can be measured, often very accurately. It is generally reasonable to deduce the total output of energy of an organism or of groups of organisms by measuring the amount of oxygen absorbed from the environment and calculating how many joules* would be available were this oxygen all used in the respiration of glucose. From the respiration of 1 g of glucose, 23.6 kJ would be made available for an organism's activities; the uptake of 1 cm^3 of oxygen at normal temperature and pressure would make available 0.21 kJ of energy.

Heterotrophes obtain their energy from their food. For animals, it is often possible to measure the amount of food eaten and the amount of faeces (undigested food remains passed out of the body) produced, and so to calculate the amount of food assimilated (absorbed into the body). The energy taken into the animal can then be calculated from the calorific value (*calor* = Latin for heat) of the food absorbed. The calorific value of organic material can be measured by burning it in a device called a bomb calorimeter and measuring the heat output. (This provides the basis for the diet charts used by slimmers!) If the calorific values of the food intake and of the faeces production are known and the oxygen intake has been measured, an *energy balance* can be drawn up:

energy balance

calorific value of food − calorific value of faeces = amount of energy *assimilated* (taken into the body)

= output of energy calculated from the amount of oxygen absorbed (joules) + X joules

assimilation

What does X in this equation mean: (a) if it has a positive value and (b) if it has a negative value?

(a) If X is a positive value, there is an excess of energy absorbed over energy used up in vital activities, so the organism can grow or can lay down food reserves or can produce reproductive bodies (eggs and sperm).

(b) If X is negative, then there is too little food being absorbed to provide the whole energy output; the animal is either living on its food reserves or is slowly dying from starvation.

For green plants, a similar balance of energy intake and use can be drawn up:

energy (from sunlight) fixed in photosynthesis = output of energy in respiration + Y joules

where Y represents energy retained in the plant either in the form of new tissue (i.e. the result of growth) or as a storage product (such as starch in potatoes). The equation is usually expressed in a different form:

gross primary production (i.e. energy fixed) = respiration + *net primary production* (i.e. energy retained)

gross primary production
net primary production

With green plants, the measurement of oxygen absorbed in respiration is complicated because, in sunlight, the plants perform photosynthesis and give out oxygen. In the dark, they perform respiration only. Gross primary production (the intake of energy) is usually measured by supplying a plant with carbon dioxide containing a known amount of gas 'labelled' with the isotope ^{14}C and

* You will find that many books and articles use calories or kilocalories (kcal) as units for energy instead of joules (the SI unit). To convert calories or kilocalories into joules, multiply by 4.2 or 4.2×10^3, respectively.

then measuring the uptake of this in light. An estimate of the respiration rate is obtained by measuring the uptake of oxygen or the output of carbon dioxide in darkness.

Thus, by measuring the intake of carbon dioxide or of food and oxygen, it is possible to draw up energy budgets with values for inputs and outputs for autotrophic plants and for heterotrophic animals. These form the basis for studies of energy flow in whole ecosystems and are essential for planning the rational management of the world's food resources.

2.2 Food webs and trophic levels

Before studying whole ecosystems, it is necessary to make some simplifications by dividing the organisms into categories. You have already met two possible categories: autotrophes and heterotrophes. The most common autotrophes are green plants. The heterotrophes include animals and saprophytes such as fungi (and many bacteria).

> Consider your own sources of food—where, ultimately, does the energy come from?

From the sun, via green plants. Your food sources include plants and animals; all the animals ultimately depend on plants for food energy, and the plants depend on sunlight.

The energy from sunlight can be followed from the autotrophic green plants, the *primary producers*, to the *herbivores* (the consumers that eat plants) and then to the *carnivores* that eat the herbivores and on to carnivores that eat the first carnivores, and so on. This sequence of events can be expressed thus:

plant → herbivore → first carnivore → higher carnivore

This is called a *food chain* and each link in this chain is a *trophic level* (from the Greek for 'food'). You should be able to think of many possible food chains. Here are three examples.

food chains
trophic levels

lettuce → snail → thrush → cat

grass → vole (small rodent related to mouse) → tawny owl

diatom (small marine plant)→copepod (small marine animal)→herring→humans

The natural situation is seldom as simple as this. Lettuces are eaten by caterpillars and people as well as by snails; tawny owls eat fieldmice and even earthworms, as well as voles, and humans are omnivorous and eat an immense variety of organisms. The real situation is a network of interlocked food chains, usually called a *food web*. But most animals have some main kind of food that they eat most of the time, so the division of these consumers into herbivores, first carnivores and higher carnivores (i.e. the use of trophic levels) is a reasonable simplification. The transfer of energy E through a food web can be expressed diagrammatically as in Figure 1.

food webs

> Will the amount of food energy consumed by the higher carnivores (E_3 in Figure 1) be equal to that consumed by the herbivores (E_1)?
>
> Not if this system represents the only source of food energy for the higher carnivores. Remember that each animal uses up energy in its vital activities; this energy is ultimately dissipated as heat and is not available to the next trophic level. So E_3 must be much less than E_1.

As a generalization, the amount of food energy available to the organisms of a trophic level seldom exceeds 10 per cent of the food energy taken in by their food organisms (in the previous trophic level); much of the rest is dissipated as heat through the process of respiration R. So, for each trophic level, energy should be shown to be lost from the system through respiration, as in Figure 2.

The food web for an ecosystem is not yet complete—

> What category of food-users are not shown in Figures 1 and 2?
>
> Detritivores (p. 10). You may also have added saprophytes and parasites.

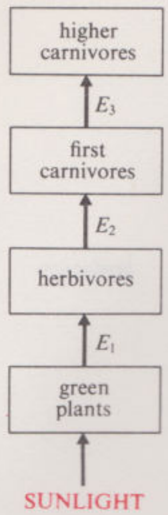


FIGURE 1 Transfer of energy through four trophic levels.

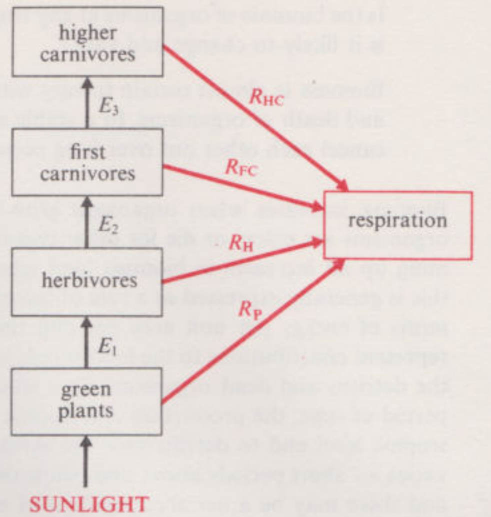


FIGURE 2 Transfer of energy through four trophic levels, showing heat loss through respiration.

During their lives, plants and animals discard organic material such as dead leaves, shed fur and faeces, cast skins (of caterpillars), and so on. Plants and animals also die for various reasons, some of which are discussed in Section 3; the dead organisms may be consumed at once, but many dead organisms are not. These dead plants and the corpses of animals, together with shed parts, form *detritus* and are the food supply for detritivores. Some of these detritivores are very specialized in their habits, as are, for example, the beetles that dispose of dung, but others consume a variety of materials. The fact that dead material normally does not accumulate under natural conditions is a tribute to the efficiency of detritivores assisted by those fungi and bacteria that are *decomposers*, breaking down dead material into simple chemical compounds. Figure 3 shows an ecosystem including detritivores and decomposers.

detritus

decomposers

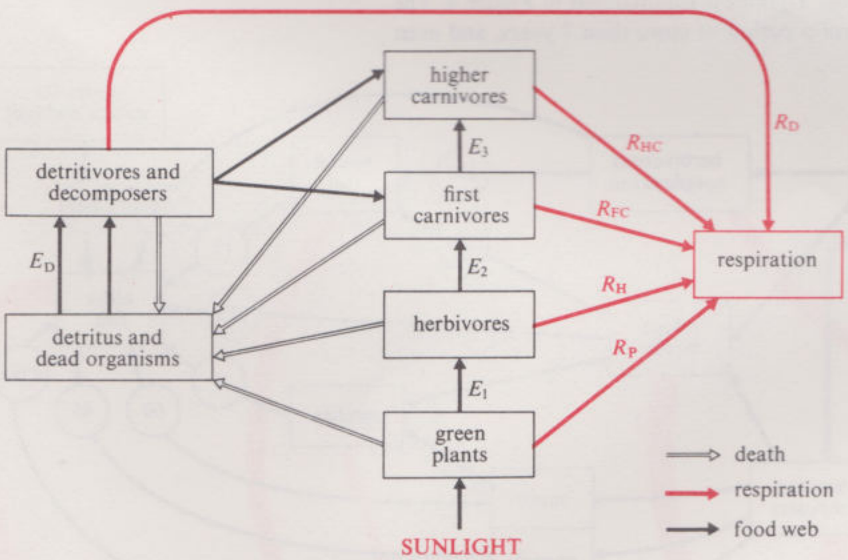


FIGURE 3 The flow of energy through an ecosystem.

Note that in Figure 3 the detritivores and decomposers are shown to respire and thus to dissipate energy; they are also shown as possible food sources for carnivores, and they themselves die and decompose.

Before studying energy flow in real ecosystems, there is yet another set of values to consider—the energy locked up at any time in the bodies of the organisms of the various trophic levels. The mass of each set of bodies is called the *biomass* of that group of organisms; we talk of the biomass of plants or the biomass of first carnivores, for example. If a representative sample is combusted in a bomb calorimeter to give a calorific value, biomass can be expressed in terms of energy—as joules. In quantitative studies, the values are often expressed per unit area of the site studied, usually as m^{-2} or km^{-2}, and averaged over a given time, usually one year but sometimes a shorter period.

biomass

Is the biomass of organisms at any trophic level likely to remain constant or is it likely to change and vary?

Biomass is almost certain to vary with time as a result of the birth, growth and death of organisms. In a stable ecosystem, these changes are likely to cancel each other out over long periods, say years.

Biomass increases when organisms grow and reproduce and decreases when organisms are eaten, or die for other reasons, or shed parts of themselves. Summing up all increases in biomass (and ignoring decreases) measures *production*; this is generally expressed as a rate of increase of biomass over a period of time in terms of energy per unit area per unit time. The decreases in biomass usually represent contributions to the food supply of the next trophic level or additions to the detritus and dead organisms. In a stable ecosystem, over a sufficiently long period of time, the production of a trophic level is balanced by losses to the next trophic level and to detritivores; the biomass can be assigned a mean level and varies for short periods above and below this. Some ecosystems are not balanced and there may be a net accumulation of energy, for instance as the biomass of tree-trunks, or a net loss of energy, as when forests are cropped for timber.

production

2.3 Energy budgets for ecosystems

To produce an energy budget for even the simplest natural ecosystem could be a mammoth task as it should involve measurements of the food consumption, respiration, growth and reproduction of a very large number of organisms. In practice, estimates are made for the organisms that appear to be most 'important', that is to have the highest biomass or the highest production at each trophic level; the error limits are often high because of the variability of the populations and the difficulties in sampling them. In this text you will study first an aquatic ecosystem and then a terrestrial one; look out for similarities and differences between them.

2.3.1 The River Thames ecosystem

An investigation of a part of the River Thames is summarized in Figure 4. The work involved nearly 20 biologists over a period of more than 7 years, and even

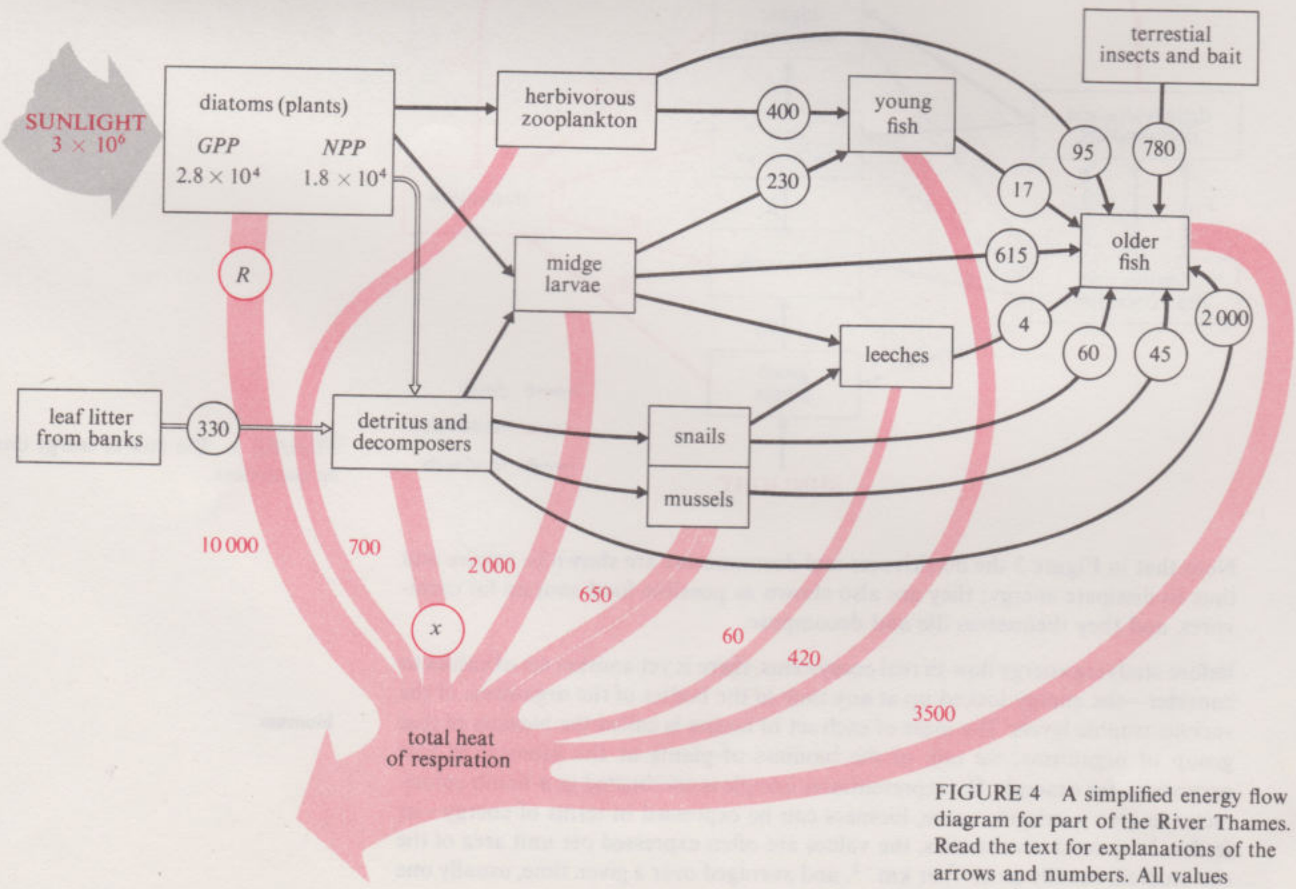


FIGURE 4 A simplified energy flow diagram for part of the River Thames. Read the text for explanations of the arrows and numbers. All values are $kJ\,m^2\,y^{-1}$.

so they were not able to quantify all the links in the food web. In Figure 4 the situation has been simplified and some energy values have been written in from other researches to give you a fuller picture. Look first at the organisms, ignoring the numbers for the moment. The principal primary producers are small plants called *diatoms* which are suspended in the water and multiply rapidly if conditions are suitable. The diatoms can also be called *phytoplankton* (from Greek 'plant' and 'roaming'); this term includes all small floating plants. They are eaten by small swimming animals called *zooplankton* (from Greek 'animal' and 'roaming'), which are similar to the 'water fleas' that you can buy as fish food at aquarists' shops. The young fish are bleak *Alburnus* and roach *Rutilus* (Filmstrip 21.1, Frame 6) less than 1 year old; midge larvae belong to an insect group called chironomids and are often very common in the silty bottoms of rivers and lakes. Water snails and freshwater mussels are molluscs; the former move over the bottom, feeding by grazing, and the latter live partly buried in mud and draw a stream of water through their bodies, extracting small particles from it. The leeches move actively over the bottom and devour midge larvae and snails.

diatoms

plankton

Filmstrip 21.1

Now consider the energy flow in this ecosystem.

The energies in Figure 4 are all measured in kJ $m^{-2} y^{-1}$ and are mean values. The black arrows indicate food links and the numbers in circles show the amount of food consumed via that link. The red pathways show heat dissipated through respiration by the various categories of organisms; actual values are written beside the pathways. The large grey arrow shows the mean total energy in the sunlight falling on one m^2 of river during one year. Two open arrows are shown; these indicate dead material forming detritus in the river. Notice that there is an input from the trees along the bank in the form of leaf *litter* (a technical term for the dead parts of plants which reach the ground). There should be other arrows like these from all the other categories of organisms to represent dead organisms joining the detritus; these have been omitted to keep the diagram more simple. This part of the Thames is heavily fished by anglers (who return captured fish to the river) and the older fish have a food input in the form of bait (bread and maggots) as well as terrestrial insects that fall onto the surface of the water. This input is shown in the top right-hand corner.

litter

Now examine Figure 4 and answer the following questions; do not spend a great deal of time on them, but read all the answers carefully.

1 What are the sources of energy input for this ecosystem?

Three sources are shown: sunlight (3×10^6 kJ $m^{-2} y^{-1}$); leaf litter from the banks (330 kJ $m^{-2} y^{-1}$); and terrestrial insects and fishermen's bait (780 kJ $m^{-2} y^{-1}$). Sunlight is by far the greatest source.

2 What proportion of the energy from sunlight falling on the water is 'fixed' in photosynthesis by the diatoms (i.e. is gross primary production *GPP*)? What proportion of the energy from sunlight is retained by the plants as net primary production *NPP*? Note that the energy used in respiration *R* by the diatoms is shown beside the red pathway.

2.8×10^4 kJ $m^{-2} y^{-1}$ of energy is fixed by photosynthesis out of the 3×10^6 kJ $m^{-2} y^{-1}$ in the sunlight; this represents 0.9 per cent. Some of the energy in the sunlight is reflected from the water surface and the rest goes to warming up the river and its bed. Net primary production (1.8×10^4 kJ $m^{-2} y^{-1}$) is only 0.6 per cent of the energy of the sunlight.

3 What are the three principal sources of food energy for the older fish? How does this differ from the food of young fish?

For older fish, the principal sources of food energy are; detritus (2 000 kJ $m^{-2} y^{-1}$), terrestrial insects and bait (780 kJ $m^{-2} y^{-1}$) and midge larvae (615 kJ $m^{-2} y^{-1}$). The young fish eat midge larvae and zooplankton but do not eat detritus or terrestrial insects. The young fish have a narrower diet than the older ones.

4 What name is given to the trophic levels of: (a) midge larvae; (b) young fish; (c) leeches; (d) older fish; (e) snails?

(a) Herbivores and detritivores; midge larvae feed on plant material both alive and dead, so they occupy the lowest consumer level. (b) First carnivores; young fish feed on the herbivorous zooplankton and midges. (c) First carnivores; leeches feed on midges and also on snails (see later). (d) First and higher carnivores and also detritivores. Recall that detritus is their principal food (see the answer to question 3), but older fish also feed on the herbivorous midge larvae and zooplankton *and* on the carnivorous young fish and leeches as well as on the terrestrial insects (some of which are likely to be carnivores). (e) Detritivores; snails feed on dead leaves and other dead plant material so, like the midges, they fill the lowest consumer level.

5 What is the minimum food intake of the herbivorous zooplankton? Assume that all the energy is assimilated (absorbed) and becomes available for activity and growth.

The respiration of zooplankton has the value 700 kJ $m^{-2} y^{-1}$ and zooplankton are a source of food energy for young and older fishes (through growth) to a total of 400 + 95 kJ; their minimum food intake must equal the total of these energy outputs, so it must be 1 195 kJ $m^{-2} y^{-1}$. As some zooplankton must die and join the detritus and some of the food they eat is passed out as faeces, their actual food intake is probably considerably more than 2×10^3 kJ $m^{-2} y^{-1}$.

6 What is the balance between food intake and respiration for the older fishes?

Adding together all the food intakes of older fishes in Figure 4 gives a total of 3 616 kJ $m^{-2} y^{-1}$; the respiratory energy for the older fishes is 3 500 kJ $m^{-2} y^{-1}$. There is thus 116 kJ $m^{-2} y^{-1}$ of energy intake not accounted for in the diagram. Assuming that this is not just experimental error, this energy could either represent dead fish material added to the detritus or reproductive products (eggs and sperm), which are the starting biomass of the young fish during the year, or fish leaving this part of the river.

7 What is the value of x (the respiration of decomposers living in the detritus)? Assume that the ecosystem is stable and in balance so that no energy leaves it as living organisms or as dead organic matter.

To find this, sum the totals for the respiration of all the other categories; this comes to 17 330 (= 1.733×10^4) kJ $m^{-2} y^{-1}$. For the energy budget to balance, and assuming there is no change in biomass, the input of 'usable' energy, that is the energy 'fixed' in photosynthesis plus any other energy inputs into the ecosystem, should be equalled by the energy dissipated in respiration. The usable energy for this ecosystem is 2.8×10^4 (total photosynthesis) plus leaf litter (330) plus terrestrial insects and bait (780) equals 2.911×10^4 kJ $m^{-2} y^{-1}$. So the respiration of decomposers, value x, should be $(2.911 - 1.733) \times 10^4$ kJ $m^{-2} y^{-1} = 1.178 \times 10^4 = 11\,780$ kJ $m^{-2} y^{-1}$.

The River Thames ecosystem outlined in Figure 4 differs from a self-contained model ecosystem in various ways: it has inputs of energy from other ecosystems (the bank and the area from which the anglers come) and some of the groups of organisms straddle several trophic levels (notably the older fishes). But this is a 'real' ecosystem and the study of energy flow through it emphasizes two important facts. First, *dead* plant material, in the form of detritus, may be a very important food source for animals, sometimes more important than living plants. Second, the *decomposers* (bacteria and fungi) may dissipate large amounts of energy (in this case, 1.178×10^4 out of a total of 2.911×10^4 kJ $m^{-2} y^{-1}$, which is over 40 per cent). This shows the importance, often overlooked, of decomposition in ecosystems.

2.3.2 The Wytham Wood ecosystem

As an example of a terrestrial ecosystem that differs somewhat from the River Thames, consider Figure 5, which shows a simplified energy flow diagram for Wytham Wood, near Oxford. This is a typical English mixed woodland (Filmstrip 21.1, Frames 4 and 5) with oak, beech and sycamores as the common trees. It

Filmstrip 21.1

belongs to the University of Oxford and has been the location of many ecological studies. Most have been concerned with changes in the numbers of various animal populations (some of these changes are discussed later). Studies of the energetics, particularly of the leaf litter and soil organisms, are still in progress, but there is enough information to construct an energy flow diagram and balance a tentative energy budget for an average year.

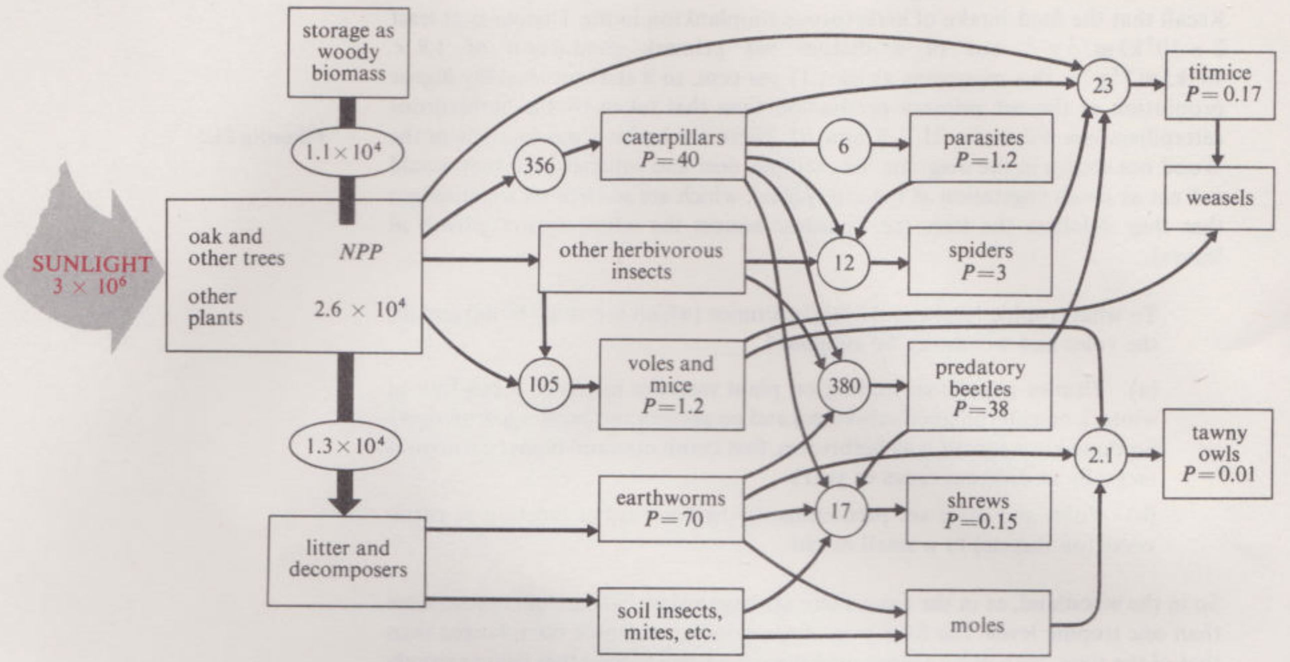


FIGURE 5 A simplified energy flow diagram for Wytham Wood. All values are $kJ\,m^{-2}\,y^{-1}$. Values inside rectangles are production P; values in circles on arrows are consumption C (for animals) or energy transfer into wood and litter.

In Figure 5, the primary producers (the plants) are at the left-hand side and their net production NPP (photosynthetic production minus respiration) is given (as in Figure 4, all values are $kJ\,m^{-2}\,y^{-1}$). The fate of this production is shown by the arrows: some is stored mainly as woody biomass as a result of tree growth; some is shed or blown down by the wind as litter; some is eaten by consumers (herbivores). The circles on two arrows indicate the amounts of primary production consumed by two types of herbivore.

The amount of solar energy falling on Wytham Wood averages $3 \times 10^6\,kJ\,m^{-2}\,y^{-1}$. What proportion of this is transformed into net primary production?

Just under 1 per cent of the solar energy:

$$\frac{2.6 \times 10^4 \times 10^2}{3 \times 10^6} \sim 0.9 \text{ per cent}$$

In the woodland, a higher proportion of the incident solar energy is transformed into net primary production than in the river (0.9 per cent compared with 0.6 per cent). The actual amount of photosynthesizing material—the leaves—is much greater in the wood but the trees include a mass of material in the trunks, branches and roots, which respire but do not perform photosynthesis. There is also a large amount of dead material in the woody parts and this is treated as stored energy in production studies; it becomes available through the activity of detritivores and decomposers when the tree eventually dies and falls down. The diatoms in the Thames grow and divide frequently when conditions are favourable but they have no way of storing production and their biomass is much less, of the order of $5 \times 10^2\,kJ\,m^{-2}$ compared with $1 \times 10^5\,kJ\,m^{-2}$ for oak-trees. So when the annual *net primary production NPP* is related to the mean *biomass B*, giving a rate of turnover of organic material, the ratio is much higher for the diatoms than for the oak-wood, because of the storage of much newly produced organic material as wood in the trees.

production and biomass

Figure 5 shows values for food consumption for some of the consumers; these are given inside the circles on the arrows. Inside some of the boxes are values for production (given as $P =$); production is a measure of all new living material produced including that eaten immediately by the next trophic level *and* that which survives, perhaps for long periods of time.

What proportion of the net primary production is represented by (a) the food consumption and (b) the production of the caterpillars?

(a) 1.4 per cent ($356\,kJ\,m^{-2}\,y^{-1}$ as a percentage of $2.6 \times 10^4\,kJ\,m^{-2}\,y^{-1}$).

(b) About 0.15 per cent (i.e. $40\,kJ\,m^{-2}\,y^{-1}$ as a percentage of $2.6 \times 10^4\,m^{-2}\,y^{-1}$).

Recall that the food intake of herbivorous zooplankton in the Thames is at least $2 \times 10^3\,kJ\,m^{-2}\,y^{-1}$ out of a diatom net primary production of $1.8 \times 10^4\,kJ\,m^{-2}\,y^{-1}$; this represents at least 11 per cent, so it is a considerably higher proportion of the net primary production than that taken by the herbivorous caterpillars (see Filmstrip 21.2, Frame 9). There are herbivorous animals in the Wood not shown in the diagram, for example, deer and squirrels; but they would not eat as much vegetation as the caterpillars, which are sometimes so abundant that they defoliate the trees (i.e. consume almost the whole spring growth of leaves).

Filmstrip 21.2

To what trophic level should (a) the titmice (which are small birds) and (b) the voles and woodmice be assigned?

(a) Titmice are shown feeding on plant material (actually beech fruit in winter), on caterpillars (herbivores) and on spiders and beetles (carnivores). So these birds function as herbivores, first carnivores and higher carnivores (actually at different times of year).

(b) Voles and mice are predominantly herbivores but function as carnivores (on insects) to a small extent.

So in the woodland, as in the river, there are organisms that can function at more than one trophic level. The food web of the woodland is more complicated than that of the river, with more species, and there are some species that belong strictly to definite trophic levels, for example the caterpillars, which eat only plant leaves, and the spiders, weasels and tawny owls, which eat only animal food.

2.4 Objectives of Sections 2.1–2.3.2

Now that you have completed Sections 2.1–2.3.2, you should be able to:

(a) Explain the meaning of the following terms: food webs; trophic levels; primary producers; consumers; autotrophes; heterotrophes; herbivores, carnivores and detritivores; decomposers; energy flow through ecosystems; gross primary production; net primary production; production of heterotrophes; biomass.

(b) Interpret a given food chain or web by stating the trophic levels of the organisms in it.

(c) Interpret a given energy flow diagram and work out consumption, assimilation, respiration and production values for the organisms in it.

To test your understanding of these Sections, try the following SAQs.

SAQ 3 (*Objective (a)*) Mark the following statements as TRUE or FALSE.

(a) Carnivores are autotrophes.

(b) Consumers and decomposers are heterotrophes.

(c) Plants are primary producers; they 'fix' some of the energy in sunlight by the process of photosynthesis.

(d) Energy flows through a community and then is recycled and flows through again.

(e) Detritivores are omnivorous heterotrophes.

(f) It is not possible to predict the production at a given trophic level from the value for the mean biomass of organisms at that level.

(g) All the net primary production in an ecosystem is immediately consumed as food by herbivores.

SAQ 4 (*Objective* (*b*)) The following may be observed on a rocky British shore, some when the tide is in, others when the tide is out:

(i) limpets grazing on diatoms attached to the rocks;

(ii) dogwhelks eating barnacles and mussels;

(iii) crabs consuming detritus and dead mussels in crannies in the rocks;

(iv) barnacles feeding on zooplankton;

(v) mussels feeding on phytoplankton diatoms;

(vi) flat periwinkles feeding on diatoms attached to seaweeds;

(vii) gulls feeding on dead crabs and mussels;

(viii) turnstones (birds) feeding on dogwhelks, limpets and periwinkles.

(a) Which of the organisms listed under (i)–(viii) are: herbivores; first carnivores; higher carnivores; detritivores; decomposers?

(b) Construct one complete food chain (this need not include all the listed species). Would it be possible to construct any other food chains? Is this ecosystem better described as a series of food chains or as a food web?

SAQ 5 (*Objective* (*c*)) The Table opposite gives values for two of three measurements for food assimilated A, respiration R and production P for populations of animals U to Z; all values are $\mathrm{kJ\,m^{-2}\,y^{-1}}$. Calculate the missing values (the blanks in the Table).

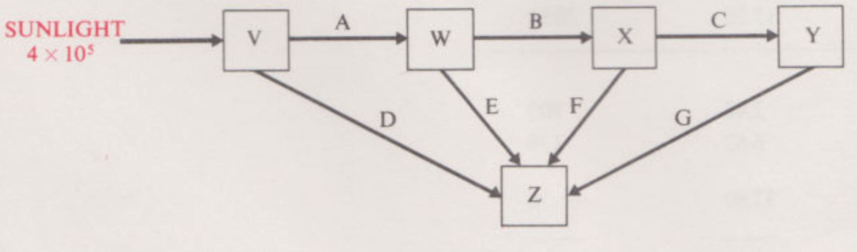
List of animals	A	R	P
U	—	68	2
V	104	78	—
W	14	—	0.2
X	—	14.8	0.5
Y	636	590	—
Z	636	—	12

SAQ 6 (*Objective* (*c*)) In a large freshwater spring in the USA, the following values were measured, all as $\mathrm{kJ\,m^{-2}\,y^{-1}}$.

	Gross primary production	Respiration	Net primary production
plants	9×10^4	5×10^4	(K)
	Food assimilated	**Respiration**	**Production**
herbivores	12×10^3	(L)	1.7×10^3
first carnivores	1.5×10^3	1.3×10^3	(M)
higher carnivores	(N)	60	40
decomposers	2×10^4	1.8×10^4	(Q)

(a) What are the values of K, L, M, N and Q?

(b) The boxes V to Z represent the trophic levels of the ecosystem in the spring. Identify each box and list the minimum values (in $\mathrm{kJ\,m^{-2}\,y^{-1}}$) of the links labelled A to G. Assume that there is no net increase in biomass and that all production not otherwise accounted for becomes detritus.



(c) Apart from the input from sunlight, is there a net import of energy into the ecosystem *or* is there a net export *or* is this a self-contained ecosystem as far as energy is concerned? If you cannot think how to answer this, identify the box labelled Z and compare the energy flow into it with the revelant values in the Table above.

2.5 The production of ecosystems

Energy studies of ecosystems are of direct interest to human populations because values for production allow the amount of human food that could be produced by different systems of management to be estimated. From the point of view of maximizing the use of solar energy for the production of food for people, we should function as herbivores and eat plants. Ideally, we should consume whole plants, choosing those that have a high net primary production and do not store much production as woody material.

At each link in a food chain there is a considerable decrease in the amount of energy available for transfer as food to the next trophic level, so a species of higher carnivore, with two or more trophic levels between it and primary production, cannot achieve as high a production as could an efficient herbivore species. But there are species of plants and parts of other plants that are inedible to humans. If there are herbivores that eat these 'inedible' plants and so make them available as human food, then it is worthwhile for people to be carnivorous and so to *crop primary production* that is otherwise not accessible. In mountainous areas, it may not be possible to grow crop plants; but sheep, feeding on the poor pastures, make some of the primary production accessible as palatable mutton.

cropping primary production

Because different plants grow in different parts of the world and the environments differ in climate and soil, primary production and plant biomass vary greatly from place to place. Table 1 gives *average* values for net primary production in different types of ecosystem and it also shows the contribution each type makes to the worlds' net primary production.

TABLE 1 Net primary production data for the world

Ecosystem	Area $10^6\,km^2$	Mean net primary production $kJ\,m^{-2}\,y^{-1}$	Total world net primary production $10^9\,MJ\,y^{-1}$
Land and Freshwater			
extreme desert, rock and ice	24	0.06	1.4
desert scrub	18	1.32	24
tundra and alpine	8	2.65	21
lake and stream	2	9.45	19
temperate grassland	9	9.45	85
woods and shrubland	7	11.34	79
agricultural land	14	12.29	172
tropical savannah	15	13.23	198
northern conifer forest	12	15.12	181
temperate deciduous forest	18	24.75	446
tropical forest	20	37.80	756
swamp and marsh	2	37.80	76
total or average	149	13.80	2058
Marine			
open ocean	332	2.42	803
continental shelf	27	6.62	179
estuaries, coral reefs and seaweed beds	2	37.80	76
total or average	361	2.93	1058
total for Earth	510	6.05	3116

Of all the ecosystems listed in Table 1, which have the highest values of annual net primary production per unit area?

Tropical forest, swamp and marsh, estuaries, coral reefs and seaweed beds are the most productive.

Some of the highest values for net primary production come from swamps where the common reed *Phragmites communis* (Filmstrip 21.1, Frames 2 and 3) grows very densely; values of 150 to 180 $kJ\,m^{-2}\,y^{-1}$ have been recorded, compared with an average value of 37.8 for swamps and marshes. This plant is not eaten by humans but can be used for thatching roofs. The high production of forests, also, is mostly in a form unsuitable for human food; it is stored as woody biomass.

Filmstrip 21.1

Marine ecosystems occupy more than two-thirds of the world's surface; how much do they contribute to the world's net primary production?

Only about one-third of the total; the open oceans are similar to tundra and alpine regions in mean annual production.

The average net primary production of agricultural land is about one-third that of tropical forest. This average for agricultural production is based on two very different agricultural systems: the subsistence agriculture practised in 'under-developed' regions and the fuel-subsidized agriculture practised in 'developed' regions. Net primary production in the agricultural systems of developed countries is approximately four times as high as that of subsistence agriculture. This is partly because higher yielding crop varieties are used in advanced agriculture, but it is also the result of an extra input of energy, used up in the manufacture and application of herbicides, insecticides and fertilizers and in the operation of irrigation systems and in other treatments. The high crop production is achieved because energy (mostly from fossil fuels) is used to create the best conditions for plant growth; the added energy is not counted against gross or net primary production and it is not available directly to the plants for primary production, because only the energy of certain wavelengths of light can be used in the process of photosynthesis. You will realize after you have read the next Section why fertilizers are important.

agricultural production and energy input

2.6 Carbon and mineral cycles

Study comment While reading this Section, you should look for the fundamental differences between the 'cycling' of elements such as carbon, nitrogen and phosphorus and the 'flow' of energy studied earlier. Note the part played in the cycles by different sorts of organism.

Energy flows through the food web of an ecosystem and is dissipated as heat as a result of respiration and so ceases to be available to organisms. If there were no green plants performing photosynthesis, production at all other trophic levels would eventually stop; you can verify this from Figure 3. In Section 2.1, autotrophes and heterotrophes are defined according to differences in the sources of the energy they need for life and growth.

In addition to sunlight, what do plants require for growth?

Carbon dioxide and water (which are the raw materials for sugars and other carbohydrates) and 'mineral salts', for example, nitrates, phosphates, sulphates. Nitrogen, phosphorus and sulphur are part of the proteins and other compounds of which living organisms consist. (You will read more about these substances in Unit 24.)

Rooted plants obtain these mineral salts from the soil—but how do the salts get into the soil?

Nitrogen, phosphorus and sulphur are obtained by animals as complex organic substances in their food; herbivores obtain them directly from plants, carnivores obtain them from herbivores, and so on. Eventually, the complex organic substances reach the soil as plant detritus, such as dead leaves, in animal faeces and as corpses of dead animals; but the rooted plants are not able to make use of nitrogen, phosphorus and sulphur in these forms. The process in which the complex substances become transformed into mineral salts is *decomposition* and it is carried out by microbes, for example bacteria and fungi.

decomposition

Some decomposers can attack dead organic material directly, but the processes of decomposition are speeded up greatly by the activities of detritivores because these animals break leaf litter and corpses into small pieces by chewing bits and by burrowing into large pieces. This gives the decomposers access to the inner material and provides much larger surface areas for microbial action. The detritivores feed in the same way as other animals, using digested food as their source of energy and chemical compounds for growth; they dissipate heat through respiration and eventually they die and their bodies decompose. The decomposers are able to break down and assimilate tough organic compounds, such as components of wood, that cannot be digested by detritivores. The decomposers also carry out chemical processes that result in *mineralization*, that is, the breakdown of complex organic substances releasing simple mineral salts that can be absorbed by plants.

mineralization

Figure 6 is a simplified diagram of the *cycling of nitrogen, phosphorus or sulphur*. Notice that the decomposers themselves may be able to take up the mineral salts.

cycling of minerals

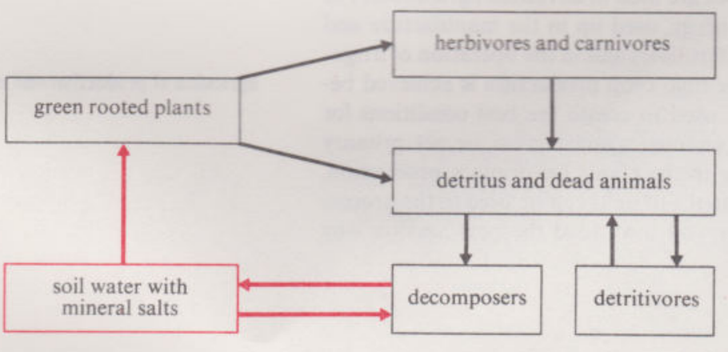


FIGURE 6 A simplified mineral cycle. Black arrows mean that the element is part of a complex organic compound; red arrows mean that the element is part of a mineral salt.

In fact, mineralization may occur in several chemical 'steps', each carried out by a particular group of microbes. To take the *nitrogen cycle* as an example, the amino acids of the detritus are first converted into ammonia (NH_3), which is rapidly converted into ammonium ions (NH_4^+) in the soil water; these are converted by one group of soil bacteria into nitrites (NO_2^-) and these are then converted by another set of soil bacteria into nitrates (NO_3^-). Most green plants take up and use the nitrates.

nitrogen cycle

> Ammonium sulphate and potassium nitrate are both used as fertilizers for crops. Which of these would be most likely to produce an immediate effect on a crop in which growth is limited by a lack of nitrogen?
>
> Potassium nitrate because plants can immediately take up the nitrate ions from the soil. Ammonium sulphate usually must be changed by the action of decomposers to give nitrate ions, so its nitrogen becomes available to most plants more slowly.

You might conclude from Figure 6 that mineral cycles are perfect, with no losses and perhaps with no gains from outside the system. This is not true.

> Bearing in mind weather conditions, suggest one way in which soils may be depleted of mineral salts.
>
> Heavy rainfall may wash salts away; this is an extreme example of 'leaching', a process that occurs as water percolates though soils, washing dissolved substances down and eventually away to sea. This commonly occurs in tropical areas when forest is cleared.

Another way in which nitrogen is lost from soil is through the activity of *'denitrifying' bacteria* which convert nitrogen compounds into the gas nitrogen (which green plants are unable to use). There are organisms that carry out the opposite process and convert gaseous nitrogen into ammonium ions; these organisms that *fix* nitrogen are found in some soils, in water, and in nodules on the roots of clovers and other legumes and also of other plants such as alder trees. Some gaseous nitrogen is also fixed by lightning during thunder storms.

denitrification

nitrogen fixation

The 'pools' of mineral salts in the soil are continually being increased through the activity of decomposers, reduced through uptake by plant roots (and some decomposers) and by leaching, and changed by the activities of other organisms that either add or remove substances. The principal elements, nitrogen, phosphorus and sulphur, are not cycled by identical processes and any one may be present in excess or may be deficient in a soil. In aquatic ecosystems, similar cycles occur; phytoplankton organisms such as diatoms take up mineral salts directly from the water and the decomposer part of the cycle may occur in the water or in the uppermost layer of the bottom sediment. Phytoplankton organisms respond to high levels of mineral salts (provided there is enough light) by producing dense growth, called 'blooms', which are a nuisance to waterworks engineers.

In agricultural ecosystems, food webs are simplified by the suppression of organisms that might compete with or prey on the food crops. The crops are removed from the land and this means that the decomposer part of the mineral cycles has almost nothing to 'work' on. This leads to a deficiency of the essential elements in the soil. Hence it becomes necessary to add *fertilizers* to enable plants to be grown. In developed countries, the fertilizers (such as ammonium sulphate, potassium nitrate and calcium phosphate) are usually produced by the chemical industry and require an input of energy from fossil fuels. In less developed countries, dung and other organic manures are carefully collected and are often the only fertilizers added to soils.

fertilizers

The element carbon is also 'cycled'.

> Remember that land plants take up carbon as the gas, carbon dioxide. How is this gas returned to the atmosphere as a result of the activities of organisms?
>
> Through the process of respiration. Recall that plants, animals and micro-organisms all respire, releasing carbon dioxide.

So the basic *carbon cycle* is very simple: the plants take up atmospheric carbon dioxide and convert it into sugars and other organic substances; animals and other heterotrophes obtain their carbon as organic substances, ultimately from plants; plants and heterotrophes return carbon dioxide to the atmosphere through the process of respiration. This shown in Figure 7. Two additional

carbon cycle

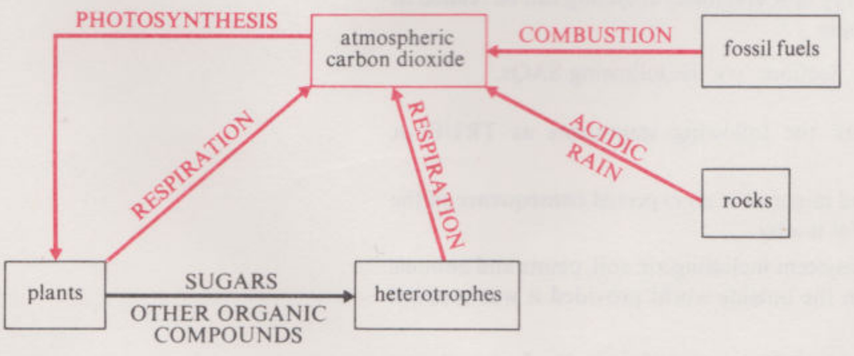


FIGURE 7 The carbon cycle. Red arrows = carbon dioxide; black arrows = organic compounds.

sources of carbon dioxide are shown: from rocks, such as limestones and chalk, exposed to heat or acidic conditions, and from the combustion of fossil fuels in open fires, factories and power stations, or in internal combustion engines. In Unit 32 this aspect of the carbon cycle will be considered further.

2.7 Niches

Study comment This short Section describes a different way of classifying the 'functions' performed by species or organisms in different ecosystems.

The division of communities into trophic levels makes it possible to draw energy flow diagrams and mineral cycles and to quantify production; but it may conceal the diversity of species and their habits within the community.

Specialized habits and activities of organisms are the basis for the concept of *niche* proposed by Elton in his classic book *Animal Ecology* in 1927. In a human community such as a town, there are recognizable niches, for example, policeman, publican and shop-keepers of different kinds. Each title conveys the function of the individual and some attributes, for example the policeman must be over a minimum height but the others could be tall or short. For animals, the niches can often be defined by size and food habits, but other habits may also be relevant. Note that the niche is the role played by the organism in its community; it is not the same as the 'habitat', which is the place where the organism lives. **niches**

When communities have been broken down into niches, the species filling these in different places can be identified and compared. Take, for example, the herbivores feeding on oak-trees. Deer occupy the niche of 'large herbivores eating oak leaves' and there is a quite separate niche of 'small herbivores eating oak leaves' occupied by caterpillars. Another herbivore niche, that of 'feeding on sap', is occupied by aphids (greenfly) and there are also herbivores living as parasites on oak leaves, producing 'galls'. Similar niches can be recognized in family gardens: human beings occupy the large herbivore niche, sometimes along with rabbits or guinea-pigs, and the small herbivore niche includes caterpillars, snails, slugs, grasshoppers and some beetles. Some of these herbivores occupy a specialized niche because they will eat only one or a few species of plant. The existence of these specialized niches allows the existence of very complex communities with large numbers of species. The examples given here are all herbivores but there are many niches in the other trophic levels, as well as further herbivore niches not mentioned here.

2.8 Objectives of Sections 2.5–2.7

Now that you have completed Sections 2.5–2.7, you should be able to:

(a) Explain the meaning of the following terms: cycling of carbon, nitrogen, phosphorus and sulphur; mineralization; niches.

(b) State the part played by different categories of organism in the cycling of carbon, nitrogen, phosphorus and sulphur in ecosystems.

(c) Show how the principles of energy flow and mineral cycling can be related to problems of producing food for people.

To test your understanding of these Sections, try the following SAQs.

SAQ 7 (*Objective* (*a*)) Mark the following statements as TRUE or FALSE.

(a) The cycling of carbon and minerals is an expected consequence of the principle of the conservation of matter.

(b) In theory, a balanced ecosystem including air, soil, plants and animals could exist totally cut off from the outside world provided it was exposed to sunlight.

(c) Mineralization is the process of conversion by plants of mineral salts into carbon compounds containing nitrogen, phosphorus and sulphur.

(d) Herbivorous zooplankton occupy a niche that is very similar to that of caterpillars on oak leaves.

SAQ 8 (*Objective* (*b*)) Which of the following types of organism are essential for the cycling of nitrogen (or phosphorus or sulphur), and why?

(i) green plants; (ii) herbivores; (iii) carnivores; (iv) detritivores; (v) decomposers?

SAQ 9 (*Objective* (*c*)) Figure 8 shows the rate of growth of a crop plant when treated with two fertilizers A and B, either together or separately. What can you deduce about the condition of the soil from these data?

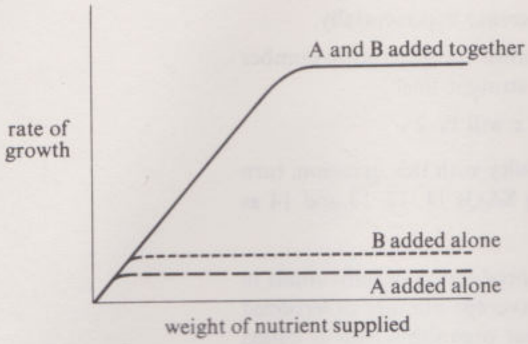


FIGURE 8 The rate of growth of a crop plant showing the effects of nutrients A and B added separately and together.

SAQ 10 (*Objective* (*c*)) Before the Second World War, it was common for farmers in Britain to follow a 'rotation of crops'. One-quarter of the ploughed area was sown with each crop and in each field there was a sequence over 4 years: root crops (e.g. turnips, mangolds); barley; clover mixed with grass; wheat. The root crops were fed to stock (cattle, pigs, sheep) during the winter, often in the field; the clover–grass mixture was either made into hay and fed to stock over the winter or was ploughed into the soil. Barley was harvested mainly for stock feeding, wheat for human food. Explain how this rotation conserved the farm's resources of mineral salts.

SAQ 11 (*Objective* (*c*)) Off the coast of Peru, there is an area of sea where there is usually a very rich growth of phytoplankton that forms the basis of the food chain:

phytoplankton → zooplankton → anchoveta (fish) → guano birds

The guano birds roost on islands and their droppings form a rock that is very rich in phosphates. There are very large numbers of anchoveta which can be caught easily in nets. Suggest two ways in which the Peruvians could exploit this marine ecosystem to increase world food supplies—which would you recommend?

3 Numbers of individuals in populations

Study comment This Section is concerned with numbers of individuals in populations and with how and why they change or vary. You should not be surprised to find that there are a number of calculations and graphs, but you should always be able to interpret them in words and you do not need to remember details. You will require your calculator to convert numbers into their logarithms. The relevance of the study of population dynamics to the control of insect pests is demonstrated in Section 3.3.1. From Section 3 you should learn the meaning of the concepts of fecundity, mortality and survival.

reproduction

The survival of a species depends on the vital activity of *reproduction*. The great majority of plants and animals reproduce sexually so, as you will recall from Units 18 and 19, their life histories start with a zygote (a fertilized egg) and, if successful, end with the new adult playing its part in sexual reproduction, either by laying eggs or by fertilizing eggs produced by another individual.

In Unit 18, you studied how population numbers can change from generation to generation with different rates of reproduction. From your memory of that Unit, answer the following question:

If an organism produces two offspring and then dies, and each of the offspring survives and produces two offspring, and this pattern continues (with all the births and deaths synchronized), which of statements (i)–(iii) are TRUE?

(i) The population of the organism would increase exponentially.

(ii) When population numbers are plotted against the generation number on a log–linear graph, the points will lie on a straight line.

(iii) The number of organisms in generation x will be 2^x.

All three statements are true. (If you had difficulty with this question, turn back to Unit 18 and revise Section 4, studying SAQs 11, 12, 13 and 14 as well as the text. Then return to this text.)

You learnt in Unit 18 that there is generally an over-production of individuals in each generation. Look at Table 2, which shows the average number of fertilized eggs produced in their lifetime by females of different organisms (this is called their *fecundity*; see Unit 18). For each population to remain stable (i.e. for the number of adults in the offspring generation to remain the same as in the parent one), on average two eggs from each female's egg production must survive to the reproductive stage.

fecundity

TABLE 2 The average number of fertilized eggs produced by each female

oyster	100×10^6
codfish	9×10^6
plaice	35×10^4
salmon	10×10^4
stickleback	5×10^2
winter moth	200
mouse	50
dogfish	20
penguin	8
elephant	5
Victorian Englishwoman	10

For each species listed in Table 2, write down the number of fertilized eggs that must die before becoming adult if the population is to remain stable; then express this number as a percentage of the total number of fertilized eggs produced (Table 3).

TABLE 3 The mortality before the adult state is reached

	In numbers	As a percentage of number of eggs fertilized
oyster	99 999 998	>99.9
codfish	8 999 998	>99.9
plaice	349 998	>99.9
salmon	99 998	>99.9
stickleback	498	99.6
winter moth	198	99.0
mouse	48	96
dogfish	18	90
penguin	6	75
elephant	3	60
Victorian Englishwoman	8	80

The numbers that die between the laying of eggs and individuals becoming adult, usually expressed as percentages, are called the *pre-reproductive mortalities* for each generation of organisms. The word *mortality* means the *rate of death*—in this case, the percentage dying over the period between egg production by the parent (P) generation and reproduction of the offspring (F_1) generation. *Survival* for the same period is measured by subtracting mortality from 100*; thus, for penguins,

pre-reproductive mortality
mortality
death rates
survival

* This is equivalent to *viability* (Unit 18).

survival to the reproductive stage is 100 − 75 = 25 per cent, and for mice it is 4 per cent. The fecundity, when expressed as a percentage of the mean adult population, is called the *birth rate* when applied to mammals and measures the inherent ability of the population to increase. The pre-reproductive mortality measures the rate of death of a generation of juveniles, that is offspring that are not yet sexually mature.

birth rates

> What is the relation between fecundity and pre-reproductive mortality in a stable population (i.e. one in which the numbers of adults remain the same in each generation)?
>
> Fecundity minus juvenile mortality should equal the number in the parent generation.

If births-minus-juvenile-deaths exceed parent numbers, there will be more adults in the offspring generation than in the parent generation. If this is repeated for several generations, then that population will keep increasing. Conversely, if births-minus-juvenile-deaths are less than parent numbers and this state of affairs persists for several generations, then that population will keep decreasing.

The birth rate and the death rate can both vary from time to time or place to place for populations of any species, but usually the death rate is more variable than the birth rate. It is conventional to express changes in population numbers in terms of mortalities; so most of what follows concerns factors that cause mortalities. Lowered birth rates can be expressed as mortalities that reduce the production of new individuals below the numbers that would have resulted had the parents attained maximum fecundity. Modern Englishwomen have a higher potential birth rate than Victorian Englishwomen (because they are more likely to survive pregnancy) but the mean fecundity is now less than 3, in contrast to the 10 in Table 2. This reduction in the birth rate (as a result of a lower conception rate) can be represented as a 'mortality' of 70 per cent due to 'the failure to produce the potential maximum number of children'.

The discussion so far has taken as the unit of time *a generation*, that is, the interval between the production of fertilized eggs by parents and by their offspring. Table 4 shows that this varies greatly with species. In practice, periods of time are generally measured as recorded by clocks and calendars, but from the biological point of view it is very important to interpret times in relation to the duration of each generation.

generation time

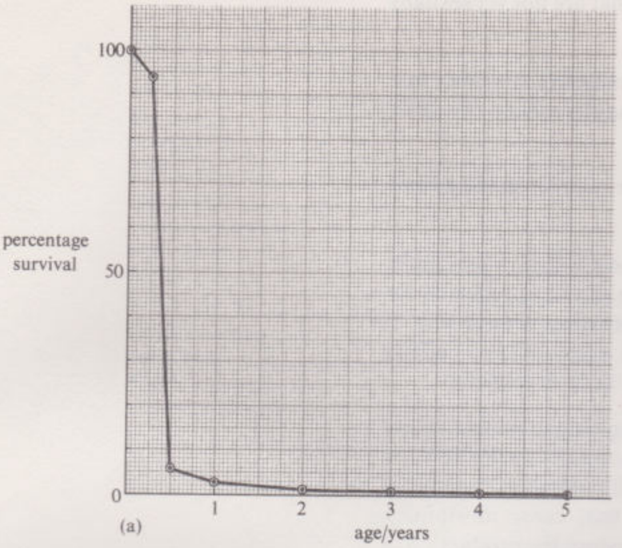
TABLE 4 Generation times for various species

Species	Generation time (average)
H. sapiens	20 years
elephant	20 years
royal albatross	10 years
codfish	6 years
salmon	4 or 5 years
great tit	1 year
stickleback	1 year
winter moth	1 year
mouse	8 weeks
Drosophila (fruit fly)	3–4 weeks

Analysing population changes is more simple when the generations are discrete than when they overlap. In Britain thousands of species of insects have an annual life cycle in which the parent generation all die before their eggs hatch into caterpillars (or other juvenile stages) and long before these are ready to breed. For many other species of insect and for most fishes, birds and mammals, the generations overlap. Adults may produce several separate broods of offspring and their older offspring may breed while the parents are still breeding. Recall as an example the marmosets discussed in Unit 18, Section 4. An analysis of a marmoset population with overlapping adult generations and a long adult life is clearly more complicated than an analysis of an insect population with discrete generations and an annual life cycle. This explains why most of the studies of population dynamics are of insect species; these studies are also important because many insects are pests. There are very few studies of plant species.

The number of survivors of a generation of offspring can be plotted on a graph against time; this is called a *survivorship curve*. Usually the actual numbers are expressed as a percentage of the original numbers, so the graphs start with 100 individuals, as in (a) and (b) of Figure 9.

survivorship curves



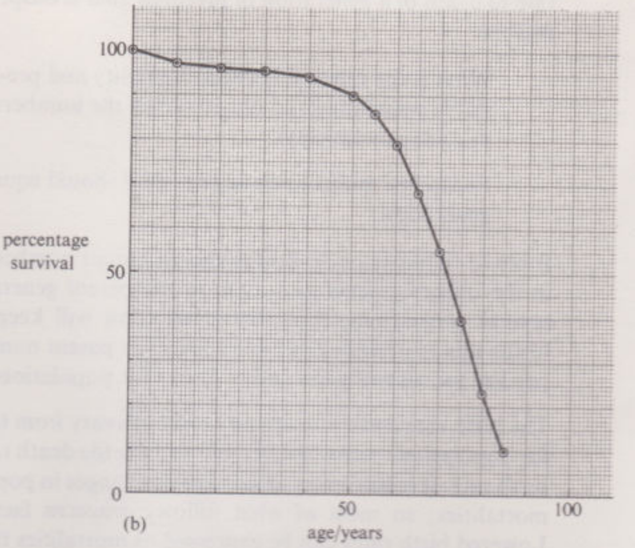


FIGURE 9 Survivorship curves for two animal species.

Match the descriptions (i) and (ii) with the survivorship curves (a) and (b) in Figure 9.

(i) The numbers fall off gradually until near the end of the life span when the adults begin to die in large numbers.

(ii) There is high mortality soon after the eggs hatch and thereafter the numbers fall off gradually; some adults live for several years.

(i) describes the curve for men (Figure 9b).

(ii) describes the curve for trout (Figure 9a).

Many species of animal suffer a high mortality early in life (e.g. the trout).

Survivorship curves form the basis for tables of 'life expectancy' such as those used by actuaries computing rates for human life assurance. Constructing *life tables* (see Section 3.2.3)—the data from which survivorship curves are drawn—is an essential step in investigating population dynamics. They make it possible to identify the ages or stages at which relatively large numbers of individuals die, that is when 'age-specific mortality' is high. Knowing these stages makes it possible to look for important causes of death and thus to deduce what factors affect the size of a population.

life tables

3.1 Population changes

Study comment This Section is important because it includes the definition of *k*-values and explains how the use of logarithms simplifies the study of population dynamics. The use of *k*-values in the analysis of causes of population change is illustrated in Section 3.2 by data from a study of tawny owls (predatory vertebrates) and in Section 3.3 by data from a study of winter moths (herbivorous insects); both studies were carried out in Wytham Wood. Look for the similarities and differences between them.

Within each generation of an animal species there is a reduction in numbers from the eggs to the breeding adults, but there are also fluctuations in numbers from generation to generation. For an example of a natural community, look at Figure 10, which shows changes in caterpillar populations on oak-trees in Wytham Wood. All the species have annual life cycles with discrete generations, and all feed at the same time of year on oak leaves. The numbers are plotted on a logarithmic scale. This is the same as plotting the logarithms of the numbers on a linear scale*. Notice that on the logarithmic scale the vertical distance between 1 and 10 is the same as that between 10 and 100, or 100 and 1 000, and that each of

HED, Section 6.9

* See *HED*, Section 6.9, if you need more information about logarithmic scales.

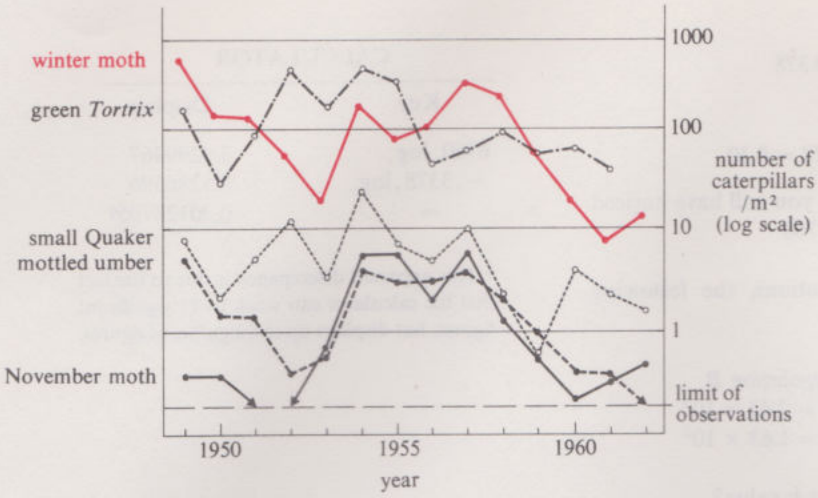


FIGURE 10 Population changes for some caterpillars on oak-trees in Wytham Wood. The numbers are plotted on a log scale.

these distances represents a ten-fold change in numbers. This type of plot means that ten-fold or one-hundred-fold changes in a very low population, such as that of the November moth, are made just as obvious as ten-fold or one-hundred-fold changes in a high population, such as that of the green *Tortrix* moth. The numbers of winter moth caterpillars vary by about one-hundred-fold over this period (between about $900\,\text{m}^{-2}$ and about $9\,\text{m}^{-2}$) and the other species show variations of the same order (more than ten-fold, usually less than one-hundred-fold); but some species are always common and others are always less numerous, for example the mottled umber and November moth. So, in addition to explaining why population numbers fluctuate, it is necessary to try to explain why some species are *common*, with high population numbers, and others are *rare*, with low population numbers.

common and rare species

J. B. S. Haldane showed that calculations involving mortality and survival can be simplified by using logarithms. Haldane represented the killing power of a mortality factor by the change in numbers caused by it, measured on a log scale; this logarithmic measure of killing power is termed the *k-value*. Each k-value is the difference between the logarithms of the numbers of individuals (usually expressed per unit area, giving population density) before and after the operation of that mortality factor. A high k-value means high mortality, that is, only a small proportion survive from the population present before that mortality occurred.

***k*-values**

To understand why the use of k-values simplifies population studies, try the set of calculations that follow.

Suppose that the population before a mortality (N_B) is 100 and the population after the mortality (N_M) is 50, it is obvious that the population was *halved* by the mortality:

$$\frac{N_B}{N_M} = \frac{100}{50} = 2$$

The k-value is:

$$k = \log N_B - \log N_M$$
$$= \log 100 - \log 50$$
$$= 0.30$$

CALCULATOR

Key	Display
100, log,	2
−, 50, log,	1.69897
=	0.30103

Now,

$$\log N_B - \log N_M = \log \frac{N_B}{N_M}\,*$$

so

$$k = \log \frac{N_B}{N_M} = \log 2$$

Check that $\log 2 = 0.301\,03$

Key	Display
2, log,	0.30103
INV, log	2

* See *HED* if necessary.

Now take another example:

$$N_B = 6\,760,\ N_M = 3\,378$$

What is the k-value?

$$k = \log 6\,760 - \log 3\,378 = 0.30$$

You will have expected this, because you will have noticed that 3 378 is approximately half of 6 760.

CALCULATOR

Key	Display
6760, log,	3.8299467
−, 3378, log,	3.5286596
=	0.30128705†

† This apparent discrepancy is due to the fact that the calculator can work to 11 significant figures, but displays up to 8 significant figures.

Suppose that for two populations, the following values are found:

Population A	*Population B*
$N_{BA} = 1.63 \times 10^5$	$N_{BB} = 7.42 \times 10^3$
$N_{MA} = 7.42 \times 10^3$	$N_{MB} = 1.63 \times 10^2$

Which mortality has the higher k-value?

To find k_A and k_B, the calculations are:

$$k_A = \log N_{BA} - \log N_{MA}$$

$$= \log 1.63 \times 10^5 - \log 7.42 \times 10^3$$

$$= 1.34$$

Key	Display	
1.63, EE, 5, log,	5.2122	00
−, 7.42, EE, 3, log,	3.8704	00
=	1.3418	00

Check that $k_A = \log \dfrac{N_{BA}}{N_{MA}}$

$$= \log \frac{1.63 \times 10^5}{7.42 \times 10^3} = 1.342$$

Key	Display	
1.63, EE, 5, ÷,		
7.42, EE, 3, =	2.1968	01
log	1.3418	00

$$k_B = \log N_{BB} - \log N_{MB}$$

$$= \log 7.42 \times 10^3 - \log 1.63 \times 10^2$$

$$= 3.871 - 2.212 = 1.66$$

Key	Display	
7.42, EE, 3, log,	3.8704	00
−, 1.63, EE, 2, log,	2.2122	00
=	1.6582	00

So, k_B has the higher value. In 'real' numbers, population A was reduced to about 1/22 by mortality A and population B was reduced to about 1/46 by mortality B.

Key	Display	
7.42, EE, 3, ÷,		
1.63, EE, 5, =	4.5521	− 02
$1/x$	2.1968	01
1.63, EE, 2, ÷,		
7.42, EE, 3, =	2.1968	− 02
$1/x$	4.5521	01

Suppose that this were a single population that suffered two mortalities sequentially (one after the other) so that $N_{BA} \rightarrow (N_{MA} = N_{BB}) \rightarrow N_{MB}$, then the total mortality K would be the sum of the two mortalities k_A and k_B. The total mortality represents a k-value of 3.00 and this is the same as $(k_A + k_B)$, that is, $1.34 + 1.66 = 3.00$. The population is reduced to one-thousandth of its original value ($\log 1\,000 = 3.00$).

Key	Display	
1.63, EE, 5, log,	5.2122	00
−, 1.63, EE, 2, log,	2.2122	00
=	3	00
3.00, INV, log	1000	

The real advantage of using logarithms is that the same proportional change always has the same k-value no matter how large or small the actual numbers in the population, and so it is easy to compare the impact of a mortality on populations of different sizes, such as caterpillars of the same species in different years.

***K* (generation pre-reproductive mortality)**

The *total pre-reproductive mortality* K is the sum of the killing powers of the mortality factors acting in succession on the population of eggs produced by the parent generation. Thus,

$$K = k_1 + k_2 + k_3 + \ldots k_n$$

where k_1 is the first mortality factor acting on the eggs and young, k_2 is the next, and so on; k_n is the last in the series of n mortality factors.

3.2 Tawny owls in Wytham Wood

A classic study of mortality factors affecting a population of a vertebrate animal is that carried out by H. N. Southern on the tawny owls of Wytham Wood. To appreciate his observations, you need to know about the life history and habits of tawny owls (*Strix aluco*). You are not expected to remember details, but you should try to understand how the numbers of owls are affected by the factors studied.

The tawny (Filmstrip 21.1, Frame 7) is the most common owl species in Great Britain, where it is widely distributed wherever there are large trees. It roosts in trees by day and becomes active at dusk; its method of hunting is to perch on a low bough of a tree and then drop onto its prey, which the owl probably usually detects by the sounds it makes.

Filmstrip 21.1

Tawny owls probably spend their whole adult lives in one area, where they hold 'territories'; each pair finds food within this territory for themselves and their young. They 'defend' the borders of the territory by threatening any other tawny owl that approaches, and the intruders usually retreat. Territorial behaviour is quite common among birds and is displayed by some other animals, for example male sticklebacks. The area defended may be just a small nesting area, as in gull colonies; but for tawny owls it is quite large and must supply food, shelter and nest sites for the mated pair.

A typical year in the life of a pair of tawny owls is as follows:

In *August* and *September*, the birds moult (i.e. they lose their feathers and grow a new set); they are silent and inconspicuous.

In *October* and *November*, each pair of birds asserts its territory. Each owl spends 15–20 minutes at dusk hooting (hōoo-hŭ-hŭ-hŭ-hōoo) from a prominent tree. Later the owls hunt for food. If an owl encounters an owl other than its mate, it challenges noisily by 'caterwauling'. The limits of the territories are established by noisy encounters between the residents.

In *December* to *February*, the owls begin their courtship. They choose a nest site, a hole in a tree; they roost together, often near the nest site. The male brings food to the female who calls softly (oo-wip) to attract him.

March to *May* is the breeding season. The female lays up to three eggs and begins to incubate (to sit on them) after she has laid one or two. After the eggs hatch, the parents feed the owlets through the rest of the summer.

For population studies, it is essential to make a census of the population at intervals to obtain values for population densities for different stages in the life history. For tawny owls, it is possible to map the territories and so obtain the numbers of adults; this is easiest in autumn when the owls 'caterwaul' at the edges of their territories at dusk. Owls nest in holes in trees but will use a suitable nesting box, which can be fitted with a mirror. They cannot 'see' red light so if a red torch is used they can be observed at night. Many of the nests can be located and the numbers of eggs laid and young hatched and fledged can be counted. A camera, its shutter and flash triggered by a bird interrupting a beam of infrared light, has been used to monitor the food brought to a nesting box and the movements of the adult birds and owlets into and out of it.

Individual birds can be 'ringed'—a numbered metal band is fixed loosely round one leg and the numbers are recorded in a central register run by the British Trust for Ornithology, British Museum (Natural History). Anyone finding a bird with a numbered ring informs this registry, and so movements of birds can be mapped and some information gathered about when and how they die.

3.2.1 Territories

Southern started his study in 1947, after a winter of prolonged frost and snow when many adult tawny owls died, probably from starvation. In that autumn, there were only 17 pairs of owls occupying territories on the estate (525 ha in area). The numbers increased gradually; in the 5 years from 1955 to 1959 (the end of the study) there were 30, 32, 32, 31 and 32 territories, suggesting that 32 is the upper limit to the viable number on this estate. The study therefore covers a period when the density of pairs of owls was increasing and then settling down at this maximum value. This is discussed later.

The boundaries of some territories remained remarkably constant from year to year. The same pair of owls was known to occupy certain territories for 7 years or longer; on average, each pair of owls occupied a territory for 5 years. In the first year or two the pair often failed to rear young, but usually they bred successfully in the later years of their occupation of the territory.

Suggest an explanation for the observations in the last sentence.

The owls feed entirely within their territories; their expertness in locating and collecting food increases as they know the territory better. Success in rearing young means that the male bird has been able to bring sufficient food to the nest both for the female while she incubates the eggs and looks after the small owlets and also for the owlets to grow and become fledged. An inexperienced male may not be able to find sufficient food for himself and his mate; the pair are more likely to be successful at rearing young in later years as the male becomes more expert.

In the light of these observations, what is a possible survival value of the owls' habit of holding territories?

The habit spaces out the owls, giving each pair an area in which they can seek food without interference or competition from other owls. As the population survives, the areas of the territories must provide adequate food for a pair of birds and their offspring in average years.

The information from Wytham suggests that smaller territories suffice in woodland than in parkland—on this estate an average of $16 \times 10^4\,m^2$ seems to be the minimum area that is adequate for survival.

3.2.2 Food

Owls are carnivores, but there is seasonal variation in their diet.

Between December and February, about 80 per cent of their diet consists of small rodents, principally wood mice and bank voles. From May to August, moles, young rabbits and invertebrate animals, such as earthworms and beetles, become the principal items in the diet. Refer to Figure 5 (p. 17) to see how these fit into the food web of Wytham Wood. Over the whole year, wood mice and voles comprise about 50 per cent of the vertebrate animals in the diet: these animals can be caught alive in traps, marked and released so that population sizes can be estimated.

Figure 11 gives the results of censuses of small rodents carried out at intervals of 6 months.

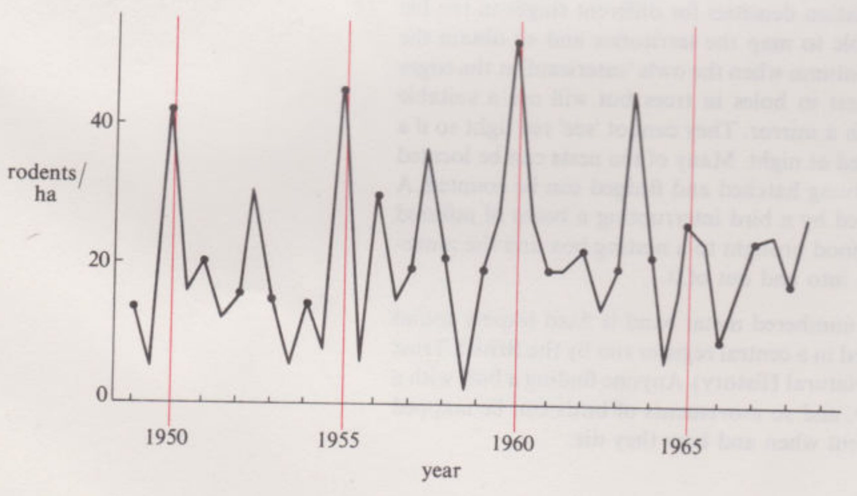


FIGURE 11 The numbers of small rodents (wood mice and bank voles) estimated at 6-monthly intervals in Wytham Wood. Dots give winter (January) values.

(a) What is the ratio of the highest number to the lowest number of these small rodents? (b) What, approximately, is the average number of small rodents per hectare ($= 10^4\,m^2$)?

(a) The lowest figure recorded is that for summer 1958, approximately 1 small rodent ha^{-1}. The highest figure is for winter 1960, approximately 50 ha^{-1}. So the highest value is about 50 times the lowest. There is no consistent pattern of changes in numbers from year to year.

(b) Approximately 20 ha^{-1}.

3.2.3 Life tables

The mean numbers of owls of different ages are given in Table 5. To draw a survivorship curve, like those in Figure 9, the data must be adjusted so that the starting number is 100; this has been done in Figure 12a. Clearly, the highest mortality occurs in the first year, so more detailed information would be useful for owls up to 1 year old. The data for 1952 are given in Table 6.

TABLE 5 Mean life table for tawny owls at Wytham. Mean number of eggs laid = 62

	Surviving at the end of the year	
Age in years	numbers	per cent
1	19	30.6
2	9	14.5
3	7	11.3
4	6	9.7
5	5	8.1

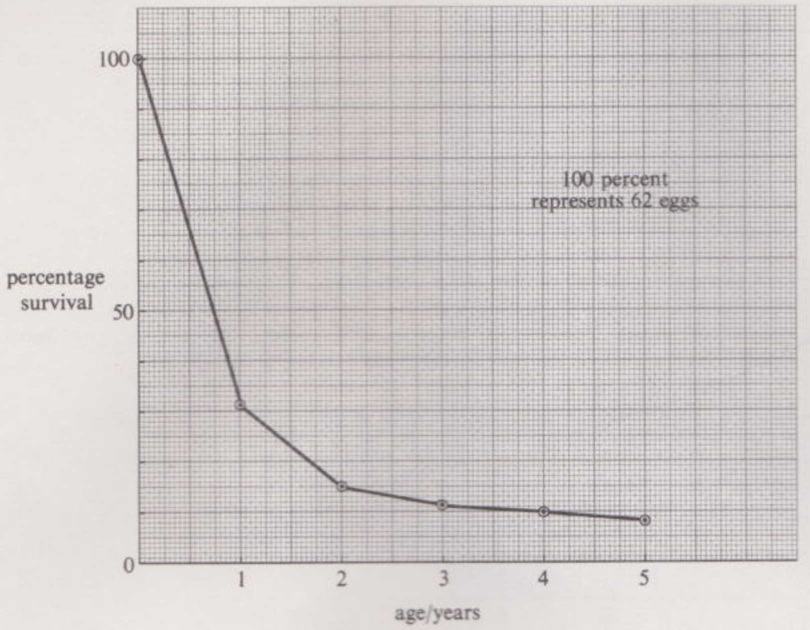


FIGURE 12a Survivorship curve for tawny owls in Wytham Wood: average life table.

TABLE 6 Survival data for 1952. Number of pairs of adult owls present = 24

	Numbers	Per cent
total number of eggs laid (March)	43	100
number hatched into chicks (April)	16	37
number of chicks fledged (June)	15	35
number of young owls able to form pairs in the wood in 1953	9	21

The survivorship curve for 1952 is shown in Figure 12b. Note that the mortality during the first year was higher in 1952/3 than for the mean life table—only 21 per cent of eggs laid survived to the end of the year compared with an average of 31 per cent. During 1952, 9 adults died so the population of adults was the same in

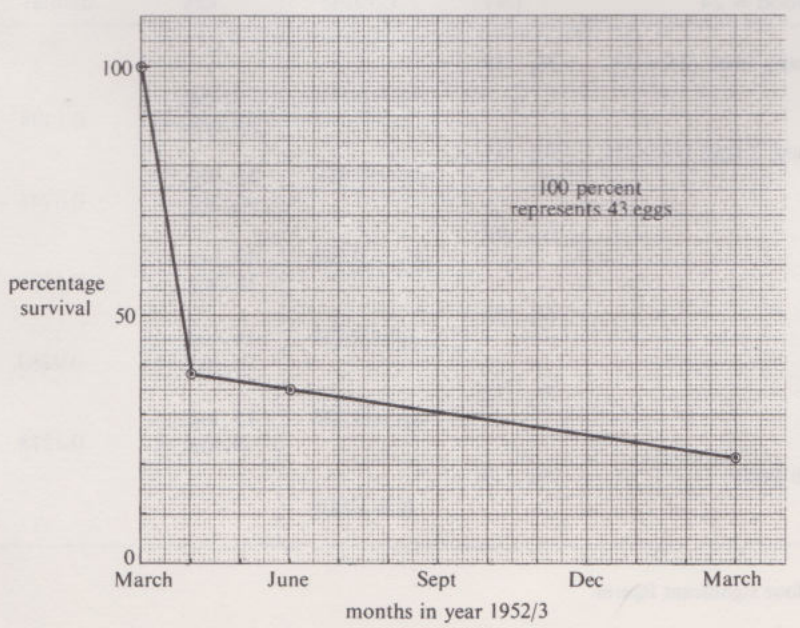


FIGURE 12b Survivorship curve for the eggs and young of tawny owls in Wytham Wood in 1952.

1953 as in 1952. The two sets of data are plotted on a log–linear graph in Figure 12c. This shows very clearly that the greatest mortality is very early in life; after hatching, the survival of chicks in 1952 was slightly better than the average survival of owls aged 1–2 years (the slope of the dashed line after April is slightly less than the full line between 1 and 2).

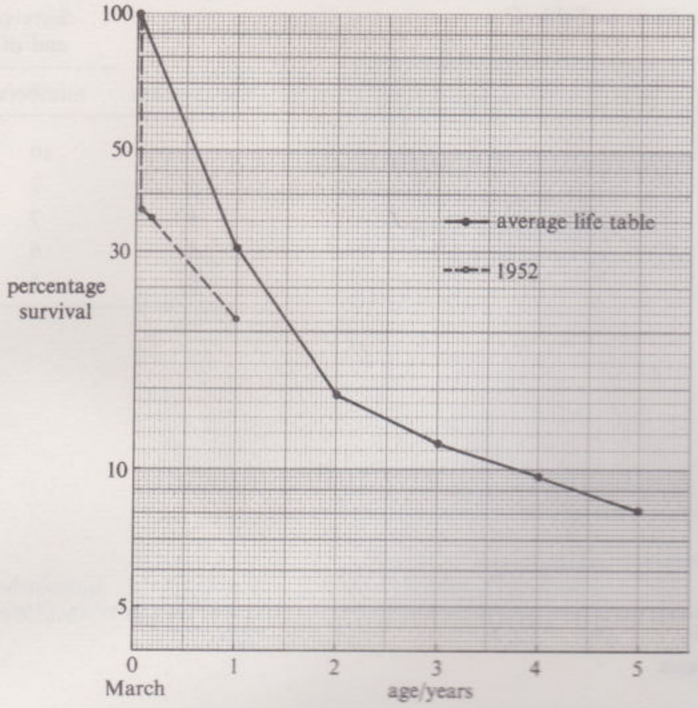


FIGURE 12c Data shown in Figures 12a and 12b plotted on log–linear scales.

3.2.4 *k*-value analysis

Each pair of owls occupied a territory for an average period of 5 years; the maximum clutch size was three eggs per pair.

From this information, calculate the value of K, the generation mortality that should result in a stable population, that is one in which each breeding pair is replaced by one pair of offspring only.

If successful, each pair will produce 15 eggs during its life-time and two of these should survive to breed. So K is found by subtracting $\log 2$ from $\log 15$: that is, $K = 0.88$.

CALCULATOR	
Key	Display
15, log,	1.1760913
−, 2, log,	0.30103
=	0.87506126

TABLE 7 Calculation of *k*-values for tawny owls in Wytham Wood

Total number of pairs of owls in the wood = 24	Number (N)		*k*-value	Calculator key	Calculator display*
maximum total number of eggs if *all* pairs bred (24 × 3)	N_1	72			
			$k_1 = 0.150$	72, log, −, 51, log, =	0.1498
number of pairs that bred = 17					
maximum number of eggs if all these laid 3 eggs (17 × 3)	N_2	51			
			$k_2 = 0.074$	51, log, −, 43, log, =	0.0741
actual number of eggs laid	N_3	43			
			$k_3 = 0.429$	43, log, −, 16, log, =	0.4293
number of eggs that hatched	N_4	16			
			$k_4 = 0.028$	16, log, −, 15, log, =	0.0280
number of chicks that fledged	N_5	15			
			$k_5 = 0.222$	15, log, −, 9, log, =	0.2218
number of owlets that survived to form pairs	N_6	9			
generation $K = k_1 + k_2 \cdots k_n$			$K = 0.903$		

* *Note* The display has been rounded to four significant figures.

Southern identified five causes of 'mortality' that act sequentially during the first year; he called them:

k_1 the number of eggs 'lost' through the failure of adults to nest or lay any eggs;

k_2 the number of eggs 'lost' through the failure of those pairs that nested to lay the maximum clutch size of 3;

k_3 the number of eggs lost before hatching; most of this loss was due to the female deserting the nest;

k_4 the number of chicks lost before fledging;

k_5 the number of young dying between leaving the nest and acquiring territories of their own in the following spring.

Table 7 shows how these k-values are calculated from the data for 1952/3 (in Table 6).

The generation K for 1952/3 (0.90) is very close to that for a stable equilibrium (0.88). Figure 13 shows K and k-values for their first year for the tawny owls from 1949 to 1959; also plotted are the total numbers of breeding pairs in each year.

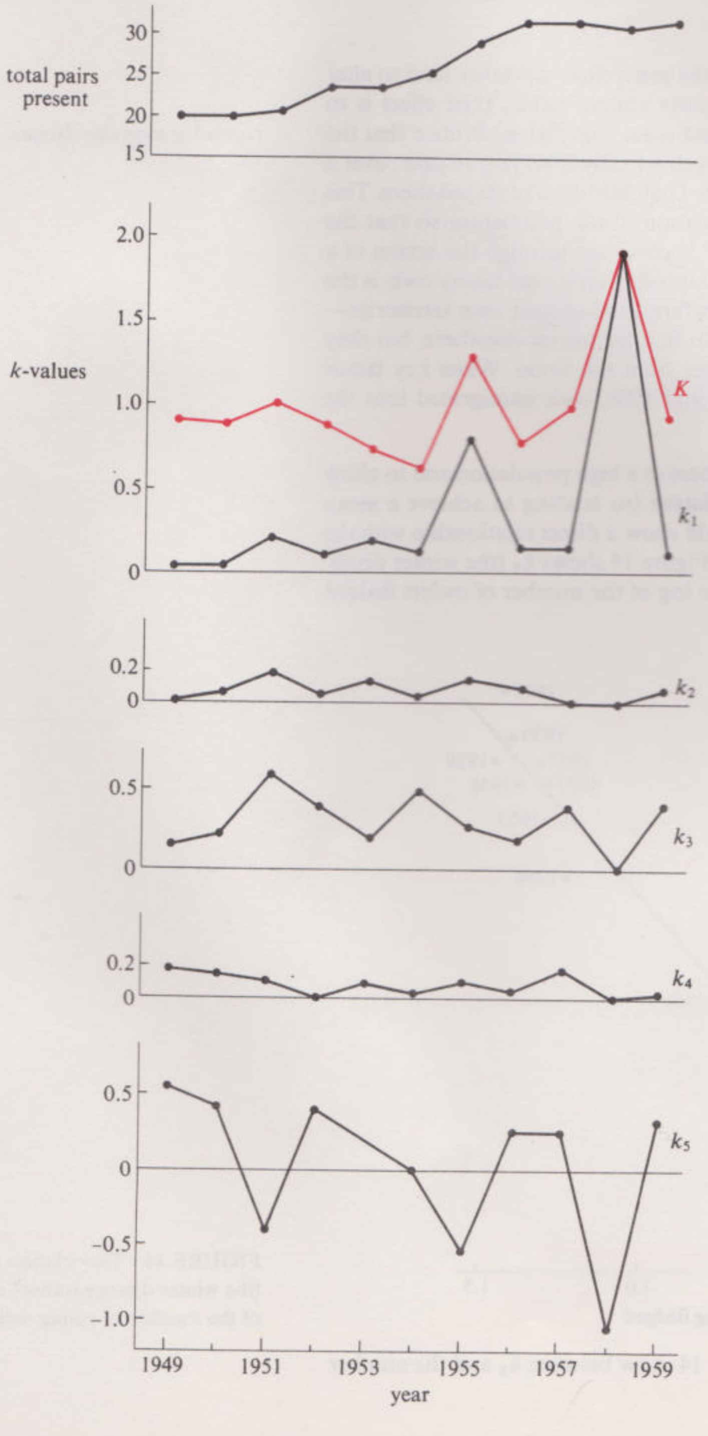


FIGURE 13 K and k-values for tawny owls in Wytham Wood.

The value of K varied between about 0.75 and nearly 2.0. In 1958, when K was highest, k_1 was very high and values of k_2, k_3 and k_4 were zero. For k_5, the value was less than -1.0; this negative value means that owlets from outside were able to immigrate into the wood and take up territories because the resident owls did not produce enough young to replace those that died. Negative values for k_5 were also recorded in 1951 and 1955.

Which of the k-values varies in the same way as K?

k_1 clearly does.

A factor that varies in the same way as K, and could therefore account for the pattern of mortality and hence for most of the change in numbers in the population at the end of each year, is called a *key factor*. For tawny owls, the *key factor mortality* in any season is the failure of adults to lay eggs at all (k_1).

key factor mortality

Do any of the k-values appear to vary in the opposite direction from K (i.e. to rise when K falls and vice versa)?

k_5 varies in the opposite way from K and reached its lowest level when K was highest, in 1958.

Factors that vary in the opposite way from the generation mortality tend to alter the numbers away from extremes and towards a mean value; their effect is to reduce population change and they are called *regulating factors*. Notice that the total population of tawny owls does not vary drastically from year to year; over a 10-year period, it rose at first and then reached equilibrium and stayed there. This stability is the result of very effective regulation of the population so that the disturbing effect of the key factor mortality is cancelled through the action of a regulating mortality factor. The regulating mortality factor for tawny owls is the death of young after leaving the nest and before gaining their own territories—actually, some of the young may emigrate to find territories elsewhere, but they are counted as dead because they disappear from the wood. When key factor mortality has been high, as in 1951, 1955 and 1958, owls immigrated into the wood from outside (k_5 was negative).

regulating mortality factors

As regulating factors act to reduce the numbers in a high population and to allow an increase in the numbers of a low population (so tending to achieve a mean population size) the regulating k-value should show a direct relationship with the density of the population on which it acts. Figure 14 shows k_5 (the winter disappearance of young owls) plotted against the log of the number of owlets fledged that year ($\log N_5$ in Table 6).

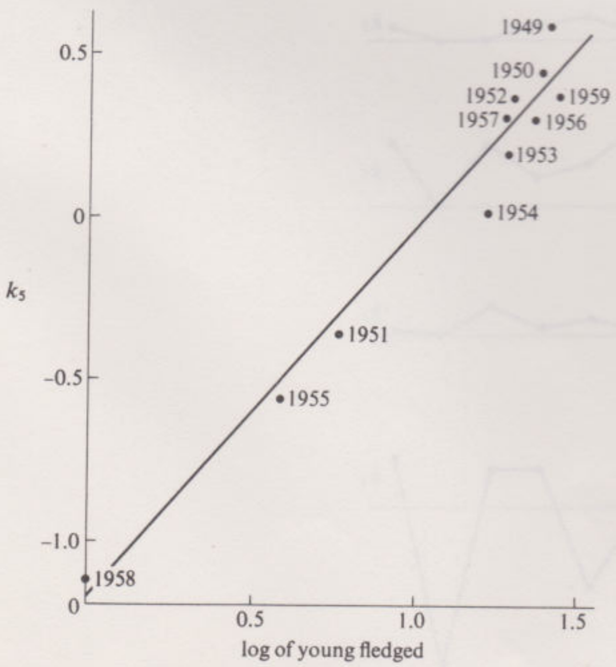


FIGURE 14 The relation between k_5 (the winter disappearance) and the log of the number of young owlets fledged.

What sort of relationship does Figure 14 show between k_5 and the number of young fledged?

k_5 is low when there are few young fledged and it is high when many young are fledged. The points lie close to a straight line.

The disappearance of young tawny owls in winter is an example of a *density dependent mortality* factor that causes relatively higher mortality in crowded populations and relatively lower mortality in sparse populations; it can regulate the numbers so that they tend towards a mean value. Key factors, which disturb the population numbers and may determine the actual numbers in any year, are usually not related to density (although they may be) but regulating factors must always be density dependent. Sometimes key factors are described as *catastrophic* or disturbing factors. The k-value analysis has shown which mortality is responsible for the fluctuations of the population numbers and which mortality acts in a way that should stabilize the numbers. Can these mortalities be related to any environmental factors that vary at Wytham?

density dependent mortality

catastrophic mortality

Consider what you have already read about tawny owls and then suggest environmental factors that are worth detailed evaluation.

(a) Variations in food supply, for example in the numbers of small rodents, might lead to fluctuations in the survival or breeding success of the owls.

(b) The English climate is very variable, so it might be worth evaluating the relation between k-values and temperature and rainfall.

(c) The number of pairs of owls on the estate rose steadily from 1947 to 1955. k_1 is lower in the early years than it is in 1955 or 1958; it might be worth investigating the relation between k-values and the density of adult owls.

3.2.5 Mortality and food supply

It is probable that adult owls died of starvation during the long snowy winter of 1946/7, just before the beginning of these observations, but Southern found no evidence of adult mortality varying with food supply between 1947 and 1959.

Figure 15 shows the relationship between $k_1 + k_2$ and the density of small rodents in June (expressed on a logarithmic scale).

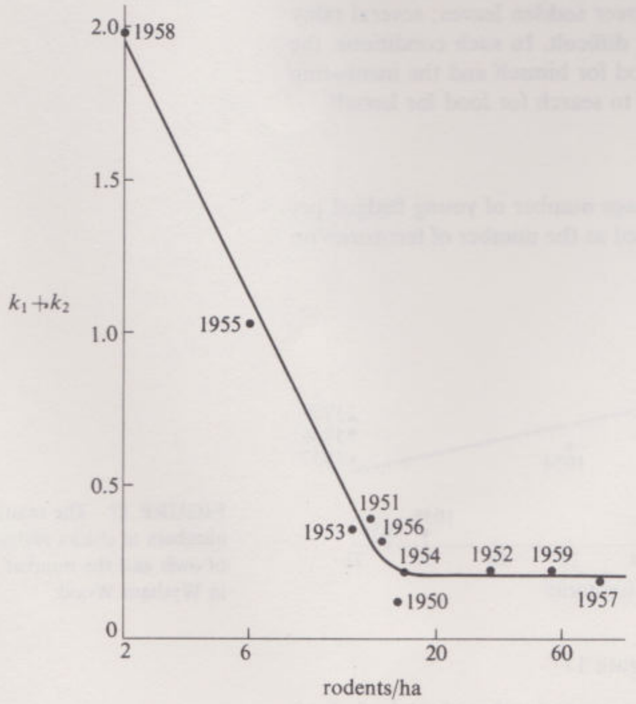


FIGURE 15 The relation between $k_1 + k_2$ and the population density of small rodents in June (on a logarithmic scale).

What conclusions can you draw from Figure 15?

$k_1 + k_2$ represents the 'losses' resulting from the failure of some pairs of owls to breed and the failure of those that bred to lay the maximum number of eggs. These losses were very high when the density of small rodents was very low in spring (in years 1955 and 1958); there is an inverse relationship

between losses and the density of rodents for rodent populations below about 15 rodents ha^{-1}. Above this value, the mortality is low and at a fairly constant level.

It seems that the breeding success of tawny owls at Wytham is dependent on the density of the rodents that are their principal food in early spring—*if* this density is less than about 15 animals ha^{-1}. Above this density, losses through failure to breed are comparatively low and independent of the numbers of rodents, even when there are as many as 70 ha^{-1}.

3.2.6 Mortality and weather

Figure 16 shows the relationship between k_3 and the number of days with 0.2 inches or more of rain in the 5 weeks after the owls started to lay eggs.

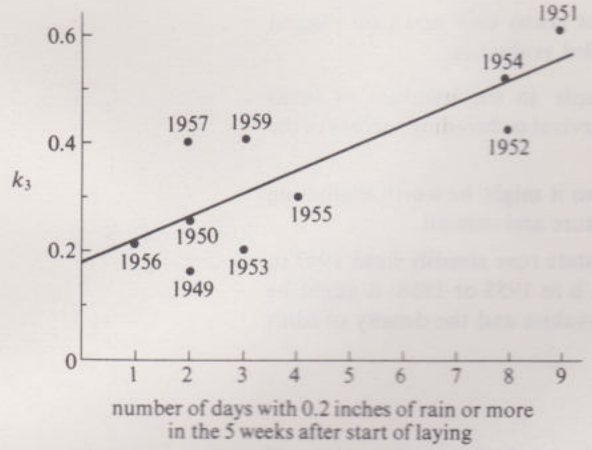


FIGURE 16 The relation between k_3 (the failure of eggs to hatch) and the number of rainy days during the incubation period.

What conclusions can you draw from Figure 16?

k_3 represents the loss of eggs before hatching; it is principally due to the failure of the female to incubate the eggs successfully. Figure 16 shows that the more rainy days there are during incubation, the greater are the losses of eggs. During nights with heavy rain, owls find it difficult to detect their prey because the animals move quietly over sodden leaves; several rainy nights in succession make hunting very difficult. In such conditions, the male may not be able to find enough food for himself and the incubating female; she may therefore leave the eggs to search for food for herself.

3.2.7 Mortality and adult population density

Figure 17 shows the relation between the average number of young fledged per territory and the number of adult owls (expressed as the number of territories on the estate).

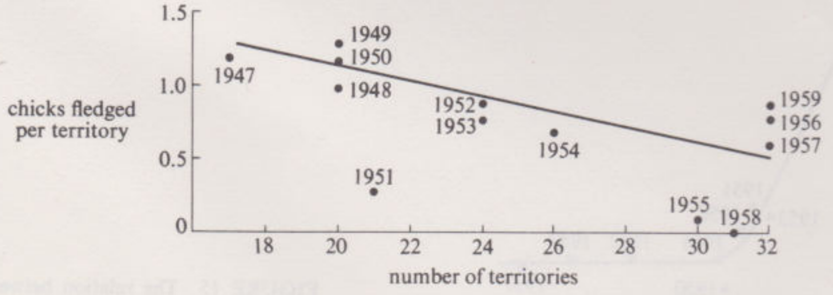


FIGURE 17 The relation between the numbers of chicks fledged for each pair of owls and the number of territories in Wytham Wood.

What conclusions can you draw from Figure 17?

As the number of territories increased, the average number of chicks fledged for each pair of owls decreased from about 1.2 (in 1947) to about 0.5 (1957). Values for 3 years (1951, 1955 and 1958) lie well below the line drawn on the graph but show a similar trend. If you check these years in Figure 11, you will find that the numbers of rodents were low in the winters. Figure 17 shows that the more adults there were, the greater the failure in breeding performance and the fewer the number of fledged young per territory.

3.2.8 Summary of tawny owl investigations

The success of tawny owls in Wytham in laying eggs, hatching them and in fledging young is determined by the general level of abundance of the voles and fieldmice that are their principal winter food supply. When these rodents are present at densities above about $15\,ha^{-1}$, the breeding success of the owls is not increased; the extra food supply does not result in extra young owls.

The key factor mortality is the failure to lay eggs. There may be an additional heavy loss due to the failure to hatch eggs because the female deserts the nest; this appears to be related to rainy weather during the incubation period. Once the young have hatched, there is a very high chance that they will survive to fledge and leave the nest.

The magnitude of the losses is usually not sufficient to reduce the number of young owlets to a point where they will replace, more or less exactly, the adults that die during a year. The regulating mortality, which adjusts the total number of adults in the estate to a definite level, acts during the winter following the fledging of the owlets; some of the young fail to secure territories and either die or emigrate. In a few years, when prey were unusually scarce, so few young were produced that there was immigration into the estate, which maintained the numbers there.

In the tawny owl populations of Wytham Wood, there are changes from year to year in birth rates and death rates.

> Is either the key factor mortality or the regulating mortality factor related to the birth rate?
>
> The key factor mortality is a reduction of the birth rate each year below the maximum fecundity. The regulating mortality factor has nothing to do with the birth rate; it depends on the ability of young owls to find territories and so avoid death.

Tawny owls are higher carnivores and, in Wytham Wood, the population of adults remains remarkably constant from year to year. There are changes in egg production (the key factor) mainly in relation to the winter food supply, and there is also a strong regulating factor caused by territorial behaviour.

3.3 Insect populations

You have seen in Figure 10 (p. 29) how the numbers of caterpillars on oak-trees in Wytham Wood may vary by up to one-hundred-fold within a 10-year period. The winter moth (*Operophtera brumata*) populations have been investigated in detail.

This moth gains its name because the adults are active on warm nights in November and December. The males have normal wings; they fertilize the eggs as the wingless females climb up the trunks of the oak-trees by night. Filmstrip 21.2, Frame 8a shows the wingless female; Frame 8b shows the winged male copulating with the female. The eggs are laid on the oak twigs and the adults die. The eggs hatch in spring, in March or April, into green caterpillars (Filmstrip 21.2, Frame 9); these feed on the oak leaves and when full-grown, usually in May, let themselves down to the ground on silken threads. They burrow into the ground and each forms a chrysalis or pupa from which the adult emerges in the following November or December. The life history is illustrated in Figure 18, which also shows how a census can be taken of the whole population twice in each generation. Females crawling up the trees can be caught in traps that resemble inverted lobster pots; in this study, each trap collected the insects crawling up one-eighth of the circumference of the tree. The full-grown caterpillars can be caught in trays of $0.5\,m^2$ area under the trees.

Filmstrip 21.2

Filmstrip 21.2

Full-grown caterpillars were dissected to give the percentages that were diseased or had been attacked by parasites, which would kill them as pupae. Another parasite attacks the pupae in the ground; it was counted by collecting adult parasites that emerged under metal trays. The eggs in some adult winter moth females were counted to give a value for fecundity.

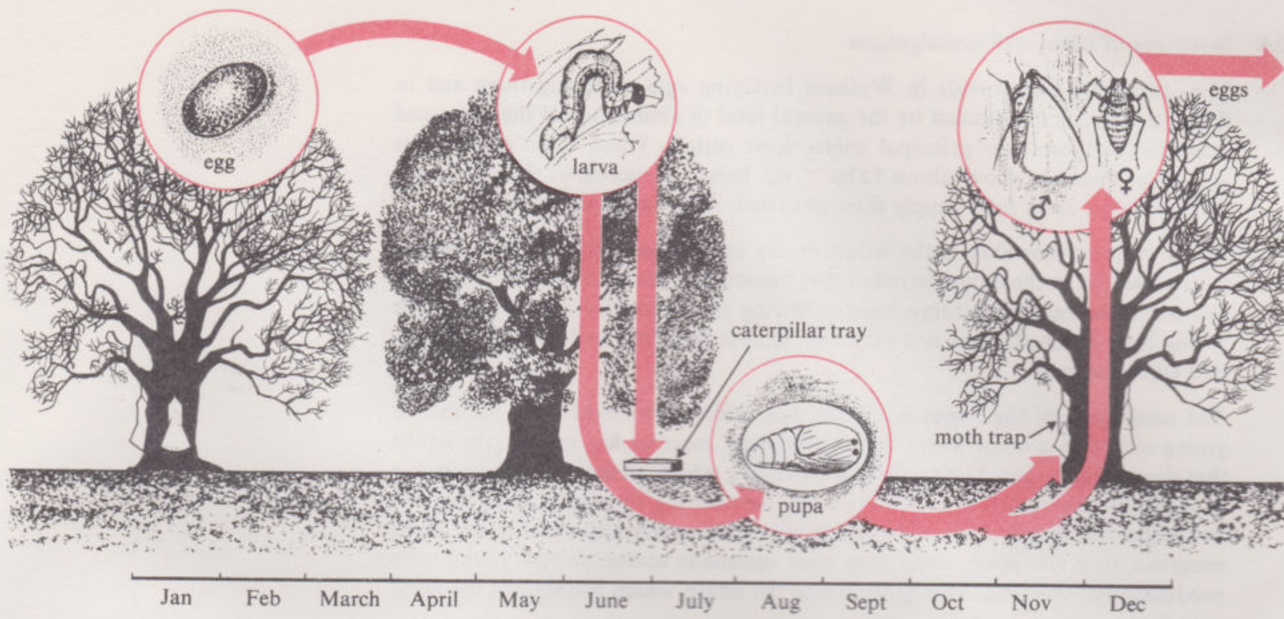


FIGURE 18 The life cycle of the winter moth *Operophtera brumata*, showing how the population can be sampled at two stages (full-fed caterpillar and female moth).

Six k-values have been calculated from the census data:

k_1 is the 'winter disappearance'—the mortality between egg production by the females in November and the establishment of feeding caterpillars in April;

k_2 is the mortality due to parasitism of the caterpillars by larvae of the fly *Cyzenis**;

k_3 is the mortality due to other parasites of the caterpillars;

k_4 is the mortality due to a disease that kills some full-grown caterpillars;

k_5 is the mortality of pupae in the soil due to predators, mainly beetles, eating them;

k_6 is the mortality due to a parasitic wasp *Cratichneumon*†, which attacks the pupae in the soil.

If you wish to have more practice in calculating k-values, try SAQ 15, which asks you to work out these k-values for the mean life-table values.

> Given that the average fecundity is 200 eggs and that winter moths live for only 1 year and breed only once, what is the value of K, the generation mortality, that would result in a stable population?
>
> Each pair of moths produces 200 eggs and only 2 of these must survive to replace their parents, so K should be $\log 200$ minus $\log 2$, which is 2.00; $\log 200/2 = \log 100 = 2$.

Figure 19 shows values of K and of the six k-values for the years 1950 to 1962. As you might expect from Figure 10, K varies considerably over the years, with values between 1.0 and 2.5.

> Which k-values vary in the same way as K? Which mortality is probably the key factor mortality?
>
> 'Winter disappearance' k_1 varies in the same way as K and is usually higher than the other k-values. It is the key factor mortality.

Variation in 'winter disappearance' is the major cause of the enormous fluctuations in numbers of winter moth caterpillars. Although part of this mortality may be due to the death of eggs, most of it occurs because very young caterpillars do not establish themselves and start to feed. The eggs hatch in spring at about the time that the buds of the oak-trees open and young leaves begin to grow. If the caterpillars hatch before the buds burst, they starve. The hatching time of winter moth eggs is almost synchronized with the bursting of the buds of oak-trees, but

* pronounced Sy-*zee*-niss.

† pronounced Krat-ick-*new*-mon.

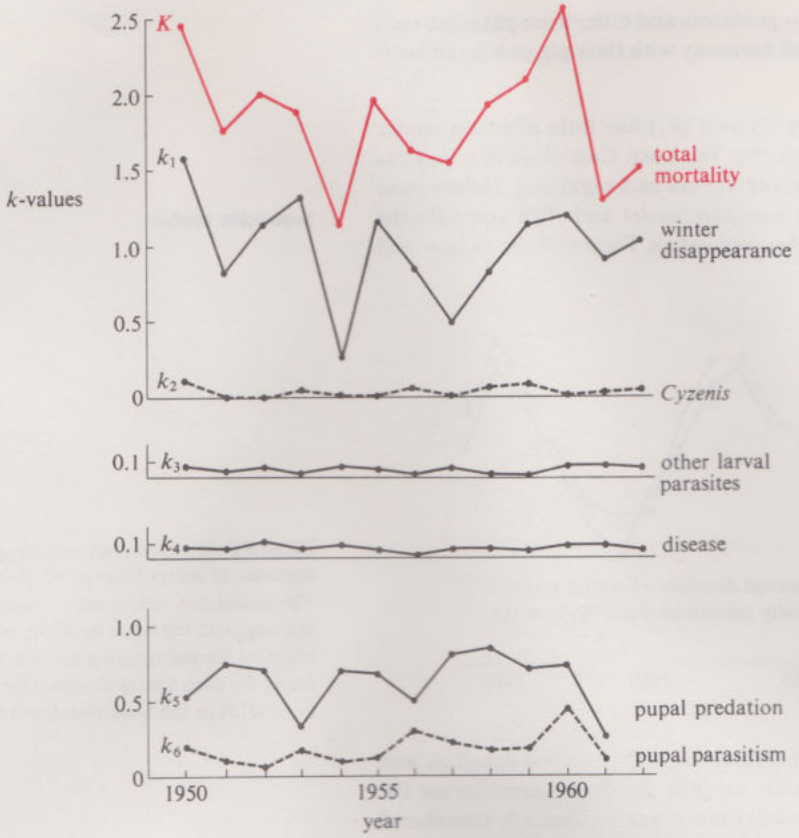


FIGURE 19 K and k-values for winter moth in Wytham Wood between 1950 and 1961.

slight differences in timing lead in some years to the very successful establishment of caterpillars, and the consequent defoliation of the oak-trees, and in other years to high mortality among young caterpillars. You may wonder why the hatching time is not delayed. If the caterpillars hatched too long after bud-burst, there would be a mortality later because the oak leaves soon become tough and loaded with bitter, poisonous substances called tannins. Many caterpillars would die from tannin poisoning before reaching the stage of pupating. So natural selection should favour winter moths that hatch just as the buds burst; the actual dates of bud-burst and of hatching vary by up to a month from year to year, depending on whether spring is 'early' or 'late'.

> Which k-values vary in the opposite way from K and k_1? Which mortality is probably the regulating factor?
>
> The most likely regulating factor is k_5, predation on the pupae by beetles and other animals.

In fact, when values of k_5 are plotted against log numbers of caterpillars ready to pupate, the relationship shows that k_5 is density dependent. So beetles and shrews eat relatively more of the pupae buried in the soil when the winter moth population is great and relatively fewer when the pupae are few in numbers; this mortality tends to bring the numbers towards the mean value. The regulation is not as effective as that of tawny owls, so the population fluctuates considerably.

Many herbivorous insects are pests of crops and trees, so trying to understand how their populations are regulated is of great practical importance. The object of pest control is to turn common insects into rare insects, so it is of interest to consider why insects such as the winter moth are common but other similar insects, for example the November moth, are rare. One likely explanation is that each has *parasites that are specific* to it, that is, they attack only that species, and that the specific parasites of the winter moth are not as efficient in finding and killing their hosts as are the specific parasites of the November moth. The most interesting parasites are flies, such as *Cyzenis*, or wasps, such as *Cratichneumon*; their eggs develop within their insect hosts and their larvae consume the host insect and then pupate to emerge later as adult flies or wasps*. As they kill their

specific parasites

* You may be lucky enough to collect or breed specific parasites of *Drosophila* in your experiments with banana mash.

hosts, these insect parasites are similar to predators and differ from parasites such as tapeworms, which may live in apparent harmony with their pig or human hosts for many years.

Key factor analysis suggests that the fly *Cyzenis* (k_2) has little effect on winter moth populations in Wytham Wood but that the wasp *Cratichneumon* (k_6) has more of an effect. A real test of whether key factors and regulating factors have been identified correctly is to set up a *computer model* and then compare the values produced by the computer with observed values. Figure 20 shows how well

population models

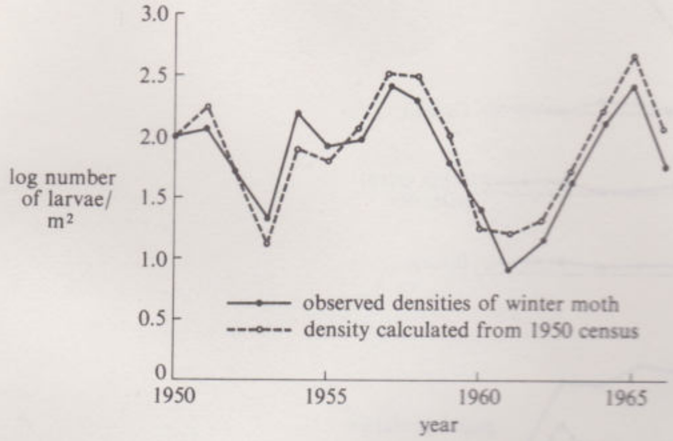


FIGURE 20 Observed and computed densities of winter moth in Wytham Wood. The calculated values were obtained by starting with the value for 1950, assuming constant fecundity, using the observed values for k_1 for each year and values for k_5 and k_6 derived from the observed density relationships.

densities of winter moth calculated from a model fit with observed densities, and this suggests that the basic assumptions are sensible. An opportunity to use the model to make predictions arose when winter moth was accidentally introduced into Canada and became a pest of forest trees and orchards. Canadian entomologists decided to attempt *biological control* by introducing specific parasites of winter moth from Europe, and they started with *Cyzenis* from England. The computer model based on Wytham Wood predicted that *Cyzenis* should establish itself and reduce the winter moth population but that there would be major outbreaks of the pest at intervals of about 10 years. The actual course of events is shown in Figure 21. *Cyzenis* established 'control' and the winter moth population

biological control of pests

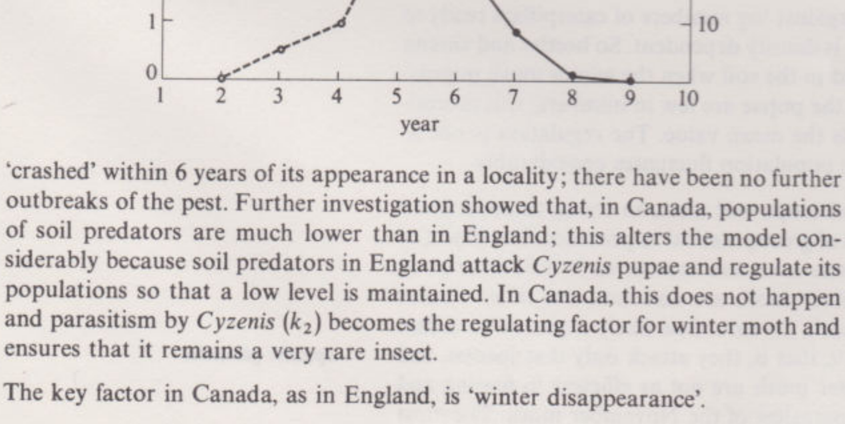


FIGURE 21 Biological control of the winter moth in Nova Scotia. Values are means for seven localities. Year 1 for each locality is the time *Cyzenis* was first observed (for most places this was 1954).

'crashed' within 6 years of its appearance in a locality; there have been no further outbreaks of the pest. Further investigation showed that, in Canada, populations of soil predators are much lower than in England; this alters the model considerably because soil predators in England attack *Cyzenis* pupae and regulate its populations so that a low level is maintained. In Canada, this does not happen and parasitism by *Cyzenis* (k_2) becomes the regulating factor for winter moth and ensures that it remains a very rare insect.

The key factor in Canada, as in England, is 'winter disappearance'.

3.3.1 Biological control

Biological control using insects that are specific parasites has two great advantages over any other method of pest control:

1 The introduced 'agents' (the parasites) will not attack any other organism.

2 Once the agent has been established, there is often no need for further action because it will continue to reproduce and to maintain its own population and that

of its host at a low level. The money spent in searching for suitable agents and then in breeding large numbers and releasing them is 'chicken-feed' compared with the money that must be spent on chemical control (with insecticides), which must be continued year after year to prevent outbreaks.

The first example of successful biological control was of a citrus pest, the cottony cushion scale *Icerya purchasi* (Filmstrip 21.2, Frame 10); this is an Australian insect that was accidentally introduced into California with citrus plants. Its natural enemies were left behind and it soon became a major pest in the new citrus plantations. An entomologist went to Australia and in 1889 sent back two species that attacked *Icerya* there. One of these, a ladybird beetle *Rodolia*, established itself and spread rapidly in California; it soon reduced the scales to negligible numbers. After the war, in the 1940s, citrus growers started to use chlorinated hydrocarbon insecticides, such as DDT, against other pests and one result was the re-emergence of cottony cushion scale as a pest; the scale seems to be more resistant to DDT than is the beetle. The citrus growers altered their insecticide programmes so that *Rodolia* survived and *Icerya* is once more a rare insect in California.

Filmstrip 21.2

Biological control is clearly an elegant way of controlling pests—and the most economical from the point of view of running costs—but the search for appropriate regulating agents may be long, and perhaps unsuccessful. Sometimes introduced agents reduce pest populations but not to a sufficiently low level. From studies such as that of the winter moth, the principles that govern the interaction between host and parasite (and between prey and predator insects) are now much better understood, so the attributes necessary for a successful biological control agent for a particular pest can be specified fairly exactly. It is difficult to use biological control for pests of annual crops in temperate latitudes, usually because agricultural practices, such as ploughing or the clearance of weeds, may prevent the parasites from completing their life cycles.

Insecticides are necessary adjuncts to agriculture but it is essential that they be used with discrimination and a clear understanding of the possible biological consequences. When the only insecticides available were substances that are dangerous poisons, such as arsenates, or else natural plant products such as pyrethrum, the use of insecticides did very little real damage to the environment. The situation was changed by the development of DDT and related compounds (in Units 16 and 17 you read about their chemistry). These are very effective against a wide range of insect species and they persist for long periods in the soil, so they appeared at first to be ideal as agricultural pesticides. It was some years before it was realized that, in addition to killing useful insects such as honey bees, they act as cumulative poisons in birds and mammals.

insecticides

> If these insecticides are used only against insect pests, how can they affect birds and mammals?
>
> There is the possibility that they could be taken in accidentally, but the real danger is that the insecticides reach birds and mammals through their normal food chains and are accumulated by carnivores, which obtain them with the herbivorous insects that are the original target organisms.

So, top carnivores sometimes have very high loads of DDT and related compounds and these reduce reproductive success and thus lead to reduced carnivore populations. When the general public became aware of this problem, there was pressure on politicians and on chemical companies to restrict the use of the dangerous wide-spectrum insecticides. At the same time, it became clear that some of the target insects were becoming resistant. DDT and some other insecticides are now banned in many countries and are generally used only after careful consideration of alternative procedures.

Another type of 'chemical control' of pests is through the use of *systemic insecticides*; these are substances taken up by a plant that are poisonous to the herbivores feeding on it, such as aphids, but do not affect any other species. Analogous with this control is the use of bacteria or viruses as insecticides; these, again, are highly specific and, although essentially 'biological', can be treated as chemical substances, stored, and used as dusts, as and when convenient or necessary. The use of insect *pheromones*, mentioned in Units 16 and 17, is another example of the employment of highly specific substances directed against one species of pest and not affecting any other organism. The practical problem is to identify and then synthesize pheromones at an economic cost.

The future is likely to see *integrated control*, a balance between chemical and biological control, with each method used where appropriate and much greater care taken not to cause indiscriminate mortality of pests, predators, parasites and animals not relevant to the problem. With a better knowledge of the life histories of the organisms involved and improved understanding of the theories of population dynamics, it should be possible to use computers to work out the likely effects of different programmes, and so to choose the best one.

integrated control of pests

3.4 Objectives of Section 3

Now that you have completed this Section, you should be able to:

(a) Explain the meaning of the following terms: birth and death rates (fecundity and mortality); life tables; k-values and K (generation pre-reproductive mortality); key factors; regulating factors; density dependent mortality; biological control of pests.

(b) Construct life tables and survivorship curves from relevant data, and interpret these by stating how mortality rates vary at different ages.

(c) Calculate K and k-values for a population from relevant data.

(d) Interpret graphs of K and k-values by stating which is likely to be the key factor mortality and which are the regulating mortality factors; given relevant data, suggest hypotheses about how these mortalities actually work (e.g. by altering the food supply).

(e) Explain the relevance of k-value calculations to the control of insect pests.

To test your understanding of this Section, try the following SAQs.

SAQ 12 (*Objective (a)*) Mark the following statements as TRUE or FALSE.

(a) If the numbers in a population are to remain stable, the pre-reproductive mortality in any generation must equal the fecundity of the parent generation.

(b) Life tables and survivorship curves always show a large decrease in numbers early in life.

(c) Key factors are always density dependent.

(d) Specific parasites each attack many different host species.

(e) k-values typically remain the same every year.

(f) Regulating factors are always density dependent.

(g) The biological control of pests is always more efficient than chemical control.

(h) A mortality is described as density dependent if it accounts for a constant number of individuals each year.

SAQ 13 (*Objective (b)*) The following figures apply to sockeye salmon in a Canadian river system. Each female salmon lays 3 200 eggs in a gravelly shallow in autumn.

640 fry (young fish, derived from these eggs) enter a lake near the shallow in the following spring.

64 smolts (older fish, survivors from the fry) leave the lake 1 year later and migrate to the sea.

2 adult fish (survivors of these smolts) return to the spawning grounds $2\frac{1}{2}$ years later; they spawn and then die.

(a) Calculate the percentage mortalities for sockeye salmon for each of the following periods:

(i) from the laying of the eggs in autumn to the movement of fry into the lake 6 months later;

(ii) from entering the lake as fry to leaving the lake as smolts 12 months later;

(iii) from leaving the lake as smolts to returning to the spawning grounds as adult salmon 30 months later.

(b) Draw two survivorship curves (one on an arithmetic scale and the other (using the actual numbers) on a log–linear plot) for the sockeye salmon in this river system. What is the pre-reproductive mortality for these sockeye salmon?

SAQ 14 (*Objective* (*b*)) (This is intended for extra practice in handling data.) Here are data for the winter moth in Wytham Wood to show the mean number of individuals killed by six mortality factors acting sequentially.

number of eggs laid by female moth	200
number of caterpillars killed by 'winter disappearance'	184
number of caterpillars killed by a parasitic fly *Cyzenis*	1
number of caterpillars killed by other parasites	1.5
number of caterpillars dying from disease	2.5
number of pupae killed by predators in the soil	8.5
number of pupae killed by a parasitic wasp *Cratichneumon*	0.5
number of adults surviving to breed	2

(a) Convert these data to show the mean numbers of individuals surviving after each mortality.

(b) Convert the mean numbers surviving into a life table, starting with 100 eggs.

SAQ 15 (*Objective* (*c*)) (This is intended for extra practice in calculating k-values.) Take the numbers of winter moth at different stages calculated in answer to SAQ 14(a) and from these calculate the values of:

K the generation mortality,

k_1 the mortality due to 'winter disappearance',

k_2 the mortality due to parasitism by the fly *Cyzenis*,

k_3 the mortality due to other parasites of the caterpillars,

k_4 the mortality due to disease,

k_5 the mortality due to predators taking pupae in the soil,

k_6 the mortality due to parasitism by the wasp *Cratichneumon*.

Refer back to early in Section 3.3 to remind yourself about the winter moth.

SAQ 16 (*Objective* (*c*)) The cinnabar moth *Tyria jacobaeae* has a single generation each year. Adult females lay eggs on leaves of ragwort *Senecio jacobaea* (a weed of pastures) in June and the caterpillars feed on the ragwort leaves and flowers. After five larval stages, the fully grown caterpillars leave the plants in July or August and pupate in the soil; the adults emerge in the following May. Some of the data from a study of a population in Norfolk are presented in Table 8.

TABLE 8 Data for cinnabar moth in Norfolk (simplified): numbers per unit area

	Year							
	1966	1967	1968	1969	1970	1971	1972	1973
number of eggs N_E	2 120	17 100	16 500	62	3 200	21 700	1 690	4 750
number of larvae at start of fifth stage N_L	730	3 440	1 940	42	2 010	2 880	269	540
number of pupae N_P	540	1 750	100	26	1 440	1 330	150	330
number of adults N_A	110	360	2	12	300	40	33	160

(a) Calculate the values of:

k_E the mortality during the egg and early larval stages ($= \log N_E - \log N_L$)

k_L the mortality during the last larval stage ($= \log N_L - \log N_P$)

k_P the mortality during the pupal stage ($= \log N_P - \log N_A$) and

K the generation mortality.

(b) From inspection of the values you have calculated, can you identify a possible key factor mortality? Go on to SAQ 17 before drawing a graph.

SAQ 17 (*Objective (d)*) The data for cinnabar moth, used in SAQ 16, were analysed in a different way by counting the numbers of larvae that died from different causes. Three main mortality factors which acted sequentially were identified.

k_M, the mortality due to mites and other animals eating the very young caterpillars;

k_S, the mortality due to starvation because the caterpillars had defoliated the ragwort plants;

k_A, the mortality due to parasitism by a wasp *Apanteles*.

(a) Figure 22 shows the values for K, k_M, k_S and k_A plotted for the years 1966 to 1973. Can you identify a possible key factor mortality?

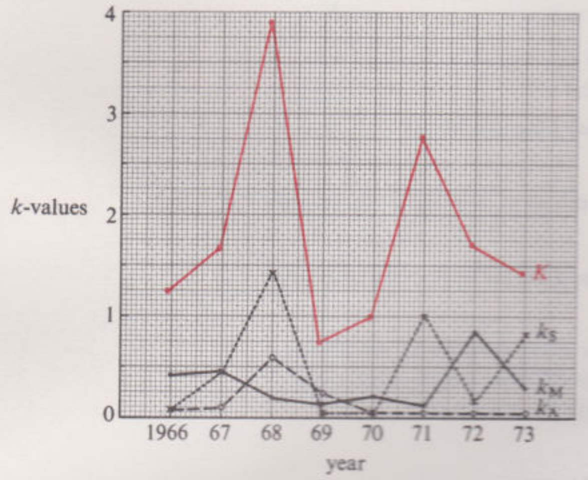


FIGURE 22 K and k-values for the cinnabar moth.

(b) On this graph, plot the values of the mortality that you identified as a possible key factor mortality in answer to SAQ 16. (Look up the values in the answer if you decided not to try SAQ 16.) Does this k-value still look as though it causes the key factor mortality?

(c) Can you identify a possible regulating mortality factor? Is this cinnabar moth population subject to strong regulation (as are tawny owls) or weak regulation (as is the winter moth)?

SAQ 18 (*Objective (e)*) Consider the relevance of population dynamics to the control of insect pests by answering briefly the following questions:

(a) What makes an insect species a pest?

(b) Do regulating mortality factors act on populations of insect pests?

(c) Define biological control.

(d) What outlay in effort is needed (i) to set up biological control and (ii) to keep it operating?

(e) How can some knowledge of the population dynamics of a pest insect in a locality where it is not a pest be useful for pest control?

(f) How can some knowledge of the population dynamics of a pest insect be helpful in planning 'integrated control'?

(g) What types of 'chemical control' avoid the indiscriminate mortality of pests and other organisms?

4 Changes in communities

Study comment This short Section is mainly descriptive; you should note the types of effect that are described but need not remember details or names of species. You need to look at Filmstrip 21.2 while you study Section 4.1.

Most ecosystems pass through sequences of changes even under conditions of stable climate and relatively little human interference. In addition to these developmental changes, there may also be gradual, long-term changes in physical

and chemical factors leading to changes in communities. Examples of these are the 'weathering' of rocks into soil and climatic variations such as the differences in mean temperature and rainfall between one decade and the next. Changes caused by human activities, called *anthropogenic changes*, include agricultural practices and the impact of recreation on environments.

anthropogenic changes

pioneer species

opportunist species

equilibrium species

A piece of bare ground is quickly invaded by plants, as any gardener knows, and an abandoned field soon becomes a 'scrub' with shrubs, small trees and tall grasses growing in it. If new bare rocky ground is formed, the rocks are soon colonized by small encrusting plants, mainly lichens and mosses; these are *pioneer* species. The pioneers include herbs (small flowering plants) which form mats over gravel or sandy surfaces. These plants cause changes in their environment, forming soils, mainly through the production and accumulation of litter. Such changes make the environment suitable for a different set of species, which take over from the pioneers. Many of these *opportunist* species are annuals (e.g. groundsel *Senecio vulgaris*) growing and flowering in one season and then dying; they often have light seeds that are blown about by the wind and they produce very large numbers of seeds. Some shrubs, such as hawthorn *Crataegus* spp.*, are opportunists, as are some trees, such as birch *Betula* spp. and sycamore *Acer*, under some conditions. A further change in soil and other environmental conditions makes the area suitable for another set of plant species. Later arrivals are usually perennial plants, many of which need damper conditions for their seeds to germinate (start to grow). Gradually, with the establishment of more species, the community becomes more complex and the opportunists disappear having been replaced by *equilibrium* plant species. These include many trees and shrubs—plants that grow large and accumulate biomass. The early communities often have spaces of bare ground between the plants but later communities typically become more and more 'closed' and the absence of bare ground is one factor that prevents some opportunist species from establishing themselves.

> From what you have just read, what sort of plant community would you expect to be the ultimate one to appear in Britain?
>
> As equilibrium species include trees, you might expect some form of woodland to be the ultimate plant community.

succession
climax community

Filmstrip 21.1

The process of change in communities is called *succession* and the ultimate stage of equilibrium is the *climax community*. This should be able to regenerate itself; the actual species present will depend on local climate and local geology. In lowland Britain, the climax community is probably usually woodland with oak as the most common tree (Filmstrip 21.1, Frames 4 and 5); in central Scotland, it is probably pine forest. In tropical areas with equable climates, the climax community is a mixed forest with a large number of species of plants, including creepers, and orchids and ferns growing high up in the tall trees. These complex plant communities provide niches for a great variety of animal species.

> Suggest how the numbers of species and numbers of individual animals might differ in an opportunist plant community in contrast with the climax community.
>
> Opportunist plants usually have fewer animal species associated with them and these species often show very large fluctuations in numbers; like the associated plants, these animals are opportunists capable of rapid reproduction when conditions are favourable. The animals of climax communities usually comprise a large number of species and their populations are often stable from year to year.

arrested and deflected climaxes

The natural succession may be deflected by natural events, such as recurring floods or fires, or by agricultural and other human activities; this results in communities that are either *arrested* or *deflected climaxes*. Section 4.1 and TV 21 consider the effects of rabbits (introduced into England as a source of human food) on plant communities, especially in Southern England. This is an example of a deflected succession; with the disappearance of rabbits, the normal succession was resumed.

* spp. stands for several species that are not given their full names here.

4.1 Rabbits

Study comment You will need to look at Filmstrip 21.2 while reading this Section.

The rabbit *Oryctolagus cuniculus* is a native of Europe that has been carried to many parts of the world because it is good to eat and carries useful fur. It breeds readily in captivity and is fairly hardy, being able to survive in central Africa as well as in the rigorous climate of Tierra del Fuego (just North of Cape Horn). Rabbits were probably introduced into Great Britain during Norman times; their close relatives, the hares, are native British species.

In medieval times, rabbits were reared in warrens as a source of food for feasts and for their fur. Some escaped and wild populations were established and spread, especially after it became common policy to reduce numbers of predators in order to protect game birds. In 1948, the annual catch of wild rabbits in England and Wales was estimated to be between 60 and 100 million animals.

Meanwhile, as shown in TV 21, rabbits had been introduced into Australia; they multiplied there and spread through two-thirds of the continent. Trapped rabbits supported an export trade, based on meat supplied to Britain and fur to the USA, worth several millions of pounds annually; but rabbits were clearly pests. They caused deterioration of pastures on a very large scale. Attempts to introduce the disease *myxomatosis*, from South America, as a form of biological control, started in 1936 and were eventually successful in 1950, when mosquitos acted as carriers transmitting the virus from sick rabbits to healthy ones.

myxomatosis

About a million square miles were infected in the first summer and there were further epidemics in the following summers with 1952/3 as the peak year. Mortality among infected rabbits was 99.5 per cent to start with but fell to less than 90 per cent by 1955, probably as a result of a change in the virus and the appearance of resistance in young rabbits. There were dramatic effects on sheep production—the increase in wool production alone was worth some £34 million; other increases in rural production brought the total profit to £50 million.

Myxomatosis was introduced into France deliberately in 1952 and spread rapidly, reaching almost every part of the country in 1953, and also the Netherlands, Germany and Spain. In Britain, wild rabbits with the disease were first seen in Kent and Sussex in the summer of 1953. The method of introduction is not known but it was not a deliberate act by anyone in authority. By the end of 1954, the disease had spread almost throughout the country. In Britain, the carrier is the rabbit flea, which breeds in burrows where the females bear and suckle their young. Some rabbits do not make burrows and nests and these are much less likely to contract myxomatosis. Refer back to Unit 20, Section 4.1, for more information about the disease in Britain and the changes that have occurred in the virus and in the rabbit's resistance to it.

What were the effects in Britain of the disappearance of almost the whole rabbit population through myxomatosis?

Rabbits are grazing herbivores as shown in TV 21 and the areas where their disappearance made the greatest impact on the vegetation are the chalk downlands characteristic of southern England. In the Middle Ages, these were grazed by sheep but in more recent times the principal grazers have been rabbits.

Would you expect the plant community of the chalk downs grazed by rabbits to be a climax community?

As grazing could prevent the establishment of tall plants, the community is likely to be a deflected climax.

Filmstrip 21.2 includes two pairs of photographs: one of each pair was taken before and one after myxomatosis had killed almost all the rabbits in that locality. Both are chalk areas. Lullington Heath, Sussex, was photographed in early spring in 1954 (Filmstrip 21.2, Frame 11) and again in 1967 (Filmstrip 21.2, Frame 12).

Filmstrip 21.2

What has changed between 1954 and 1967?

There has been an obvious change in vegetation from broken turf with bare chalk and some bushes (Filmstrip 21.2, Frame 11) to a dense sward of grass with a tangle of brambles (Filmstrip 21.2, Frame 12).

The rabbit burrows in 1954 were surrounded by areas of bare chalk with some patches of turf. The bushes near the burrows are elder *Sambucus nigra*; these plants are unpalatable to rabbits. In contrast, red fescue grass *Festuca rubra* formed a closed community in 1967 with bramble bushes *Rubus* spp.—a new plant community has grown on Lullington Heath.

Filmstrip 21.2

Old Winchester Hill was photographed in August 1954 (Filmstrip 21.2, Frame 13) and again in August 1956 (Filmstrip 21.2, Frame 14).

> What has changed in this 2-year period?
>
> The most obvious difference is the presence of yellow flowers in 1954 (Filmstrip 21.2, Frame 13) and their absence in 1956 (Filmstrip 21.2, Frame 14). Closer inspection reveals bare chalk scree in 1954, most of which has been colonized by grasses in 1956.

The tall yellow flowers are ragwort *Senecio jacobaea* which, like elder, is unpalatable to rabbits. Each ragwort plant lives for 2 years only and must grow from seed, and these seeds were able to establish themselves on exposed chalk where the ground was scratched by rabbits. After myxomatosis, plants of other species grew over the bare chalk and ragwort seeds failed to establish themselves in the face of this competition.

chalk downs

The plants of the *chalk downland* of 50 years ago usually formed a community with leaves close to the ground; often they had attractive flowers, for example thyme. Absence of grazing allowed faster growing shrubs and herbs with leaves further from the ground to spring up and overshadow the traditional downland plants. The conservation of the original attractive community, the deflected climax, requires active management; people now work to clear the scrub of brambles and hawthorn or pay farmers to graze sheep on chalk Nature Reserves.

Filmstrips 21.3 and 21.4

Filmstrips 21.3 and 21.4, which illustrate TV 21 include photographs of chalk grassland plants and of plants associated with rabbits (burrows and grazing).

Biologists had realized before 1954 that the activity of rabbits was important in determining the composition of certain plant communities. When small areas of land were enclosed with rabbit-proof netting, plants appeared that did not grow outside. But the almost complete disappearance of rabbits led to much greater changes in vegetation than most biologists expected.

In addition to changes in vegetation, there were, as you might expect, some changes in animal populations, especially of those species that ate rabbits or competed with them for food. Hare populations increased steadily after the rabbits disappeared. Foxes and other carnivores switched their diets to take larger numbers of voles and mice; some lowland foxes probably also took increased numbers of poultry and game birds. There was no evidence that foxes suffered any mortality or even lost much weight when they lost an important component in their diet; they were sufficiently versatile to exploit other food sources.

These observations on the impact of myxomatosis on rabbits and the resulting changes in plant communities illustrate how alteration of part of the structure of a community may be followed by far-reaching and unpredicted changes.

Both the introduction of rabbits and their disappearance were human actions causing widespread effects on plant and animal communities.

4.2 Objectives of Section 4

Now that you have completed this Section, you should be able to:

(a) Explain the following terms: succession; climax community; pioneer, opportunist and equilibrium plant species.

(b) Suggest, or select from a list, the types of change in plant communities that might result from changes in environmental factors, and give reasons for your suggestions.

(c) Suggest, or select from a list, the factors that should be investigated before a given foreign species or a given chemical substance is introduced into an environment.

To test your understanding of this Section, try the following SAQs.

SAQ 19 (*Objective (a)*) Mark the following statements as either TRUE or FALSE.

(a) Climax vegetation includes many pioneer and some opportunist plants.

(b) During a succession, opportunist plants replace pioneers as a result of changes in the environment brought about by the pioneers.

(c) Equilibrium plant species must be able to compete successfully with many other species.

(d) During the early stages of a succession, the species must be able to survive under conditions in which the physical and chemical environmental factors are more extreme than in the late stages of a succession.

SAQ 20 (*Objective (b)*) Suppose that heavy rain, combined with an earth tremor, leads to a landslip over 2 km of a hillside in Britain, exposing a strip 250 m wide, mainly of bare rock but with some sand and gravel in depressions. Predict *in general terms* what kinds of plants are likely to grow in this new habitat in the following year. What changes are likely to take place over the following 50 years? Assume that there will be no human interference and no further landslips.

SAQ 21 (*Objective (c)*) Suppose that you were in a position to decide whether or not a certain foreign species should be introduced into this country, what types of information would you wish to have available before giving permission for its introduction? Consider this problem with special reference to:

(a) *Reindeer* These live in Scandinavia, feeding on a lichen, which also grows on Scottish mountains; they are peaceful large herbivores that live in herds and are domesticated in Scandinavia.

(b) *Canadian pondweed* This plant grows in slow-flowing and in still waters; it has long stems with many small leaves and it grows readily from short pieces. It has no need to become rooted or to flower.

(c) *Colorado beetle* This is a brightly coloured red and yellow beetle that feeds on potato plants all through its life. It is a native of the USA but is widely distributed now in Europe.

5 Human effects on ecosystems

Study comment This final Section is concerned with human population numbers and with human food supplies, both from the ecological point of view. You should note how some of the principles discussed in earlier Sections can be applied to populations of *Homo sapiens*.

In pre-agricultural times, human diets consisted of berries and roots and various animals killed for meat. An omnivore with a wide food range can readily adapt its diet to changes in the numbers and abundance of food organisms and so does not eat out any one food species.

The development of agriculture implies very considerable interference with natural ecosystems. The climax vegetation is destroyed and replaced by a monoculture; a field of one species such as wheat or cabbages replaces a forest containing oak, ash, hazel and many other plant species.

Recall from Section 2.6 the effect on soils of growing the same crop for several seasons in succession. How is this problem solved?

The yield of the crop may fall off because some essential substance is removed from the soil and not restored because the normal mineral cycle is broken. The remedy is usually to apply fertilizers; the problem can be avoided or reduced by crop rotation.

The use of fertilizers in unnecessarily high amounts has led to the problem of 'eutrophication' (enrichment) of waters because the excess fertilizer is drained from the land and promotes excessive growth of plants in watercourses.

Another result of mono-culture is the emergence of two types of biological problem organisms: weeds and pests (though the latter term may be used to include the former). Insects as pests, and possible methods of control, have been discussed earlier, in Section 3.3. Most *weeds* are opportunists; they usually grow quickly and flower early, and many are annuals. They are naturally adapted to take advantage of the 'gaps' in normal communities where the soil is exposed and there is plenty of light. There are other weed species that seem to have evolved in parallel with cultivated plants; they have no known 'wild' habitat.

weeds

5.1 Human populations

The rapid increase in human population, sometimes described as 'the population explosion', is a recent phenomenon. The change from hunting and gathering to farming probably happened in about 9000 BC and the 'industrial revolution' in Europe began in about 1750 AD. The human population was about 1×10^9 in 1830 and had reached about 2×10^9 in 1930. It almost doubled between about 1920 and 1970 (an increase from about 1.86×10^9 to about 3.66×10^9); the present trends suggest that it may double again by about 2005 AD. But to understand what is happening, it is necessary to look more closely at *human birth and death rates.*

human birth rates and death rates

Table 9 gives some information extracted from the *Demographic Yearbook 1970* published by the United Nations; the regions in this Table were chosen to illustrate the extremes of recent population changes.

TABLE 9 Data for the period 1965–1970 for selected regions

Region	Birth rate (per cent)	Death rate (per cent)	Annual rate of increase (per cent)
Central America	4.4	1.0	3.4
Northern Africa	4.8	1.7	3.1
Western Africa	4.9	2.4	2.5
Northern Europe	1.8	1.1	0.6*
Western Europe	1.7	1.1	0.8*

* includes natural increase *and* migration.

(a) Compare the birth rates for the five regions.

(b) Compare the death rates for the five regions.

(a) The birth rates in Central America and the African regions are more than twice as high as those in the European regions.

(b) The death rates for Central America and the two European regions are very similar, but those for the African regions are much higher, especially the rate for Western Africa which is twice that for Europe.

These five regions illustrate how and why the human population increase has occurred. Before 1700 AD, birth rates were probably high everywhere—but so were death rates, and the population increased very slowly. Then advances in medicine led to a decrease in the death rate, allowing a rapid increase in population because the birth rate remained high (the two African regions and Central America illustrate this second phase of population change). It seems that the European regions have progressed to a third stage in which the birth rate has decreased, and this results in a comparatively low rate of population increase. Demographers (students of human population trends) suggest that this will happen eventually all over the world and the population explosion will then be halted.

Some of the effects of increased population and the development of industrial societies can be classed under the general heading of 'pollution'. With increasing awareness of the problems and with improved technology, most pollution could now be reduced or prevented—but at a cost. The problems become economic and political.

Other human effects on the environment arise simply as a result of the large numbers of people present; these are problems of food and living space, problems that can affect all species of animals. When wild animals become overcrowded, a crash in population can result from epidemic disease or because some important food resource is eaten out. Human technology may be able to prevent these types of disaster.

5.2 Human food supplies

The problem of food supply has been much discussed, though there remain two contrasting points of view. Many agriculturalists optimistically believe that, with the use of fertilizers, herbicides and pesticides, the world can produce enough food even for the enormous population predicted for the next century. On the other hand, many ecologists and others, knowing that at least one-third of the population of the world is at present underfed, do not believe that it will be possible to produce enough to feed adequately the probable population of 30 years ahead. The estimates of these two groups of scientists differ widely; here we can only draw attention to the sort of problems that are relevant. Even the problem: 'How much and what type of food does a person need for life above the survival level?' is not easily answered. The amount needed depends on age, size and physique as well as on the level of activity and traditional eating habits.

Because of the variation among individuals and the variation in estimates of need, it is quite difficult to decide how much of a food gap exists at present. There is a high loss of food between its source of production and the people who consume it: some of this loss, particularly that due to pests of stored products, could be avoided. Waste of food for economic reasons, such as the high cost of transport, and for political reasons, as with the EEC 'mountains', are not ecological problems and require political solutions.

Apart from agricultural crops and domesticated animals, there are other sources of food: populations of wild animals in the sea are exploited by modern 'hunting' techniques. Some of the problems of maintaining optimum yields of fish without damage to the breeding stock are discussed in Radio 11. Careful manipulation of fishing effort is needed so that the numbers and sizes of fish caught are regulated. This requires international cooperation, but unfortunately this seems very difficult to achieve. Farming of marine fishes is developing but could never produce the yields that are possible from the proper management of wild fish populations. Proteins can be extracted from leaves to provide a nutritious diet that needs little supplementation; a bacterium converts petroleum into protein that can then be harvested; biochemists could produce synthetic foods. All these sources can be exploited only through manufacturing processes that use energy. The manufacture of synthetic fertilizers requires an input of energy, so the increased use of fertilizers in agriculture means faster consumption of the world's reserves of fossil fuels and so does the sustained use of insecticides and herbicides. The machines that apply these substances to the land and those that collect and process the crops also use considerable quantities of fossil fuels. Feeding the world's population uses up a great deal of energy.

As the reserves of fossil fuels are being depleted rapidly, it will be essential to develop new sources of energy, such as geothermal, tidal or nuclear energy or some process for using the solar energy at present wasted. A new source of protein obtained by a process based on one of these types of energy could make it feasible to feed three or more times the present human population of the world. The limit to population increase might then be set by density dependent physiological or behavioural reactions such as can be observed operating for other species of animals. At present very little is known about such reactions in human populations.

5.3 Objectives of Section 5

Now that you have completed this Section, you should be able to:

(a) Explain how agricultural ecosystems differ from natural ecosystems; define the terms 'weed' and 'pest'.

(b) Explain the observed changes in numbers of human populations and discuss possible future trends.

(c) Give examples of the impact of human activities on the environment and be prepared to argue about the merits of proposed conservation measures on *ecological grounds*.

To test your understanding of this Section, try the following SAQs.

SAQ 22 (*Objective* (*a*)) Mark the following statements as either TRUE or FALSE.

(a) Agriculture is based on mono-culture, which is contrary to the natural development of plant communities.

(b) Most weeds are plants that grow and reproduce themselves slowly.

(c) Pests are usually carnivorous animals.

(d) Biological control typically involves using organisms that are specific predators or parasites on pests.

(e) Persistent insecticides are the best agents for controlling pest insects.

SAQ 23 (*Objective* (*b*)) The proportion of the total population (as percentages) that fall into three separate age groups for three countries are:

	Age group		
Country	14 years or younger	15–39 years	40 years or older
Canada	33	35	32
France	24	35	41
Iran	46	34	20

By referring to Table 9 on p. 51, suggest what the birth and death rates have been in these three countries over the last decade (10-year period). What trends would a demographer expect to observe in these countries over the next 25 years?

SAQ 24 (*Objective* (*c*)) In 1965, the world population of grey seals was estimated as 46000; of these, 36000 live around the British Isles. About one-tenth of the British grey seals are based on the Farne Islands (off the coast of Northumberland) for which the following figures are available:

the number of calves produced annually was about 100 in the 1930s; about 600 in 1952; and more than 1000 in 1962;

the seals 'calve' on four islands only—here is information about two of these islands—Staple and Brownsman.

	Staple	Brownsman
number of calves per 100 yds of accessible beach	77	14
percentage of calves dying during:		
first half of breeding season	16.4	8.7
second half of breeding season	26.4	11.8

Seals are unselective carnivores, their diet includes the following species of fish: salmon, cod, plaice, sand eels, lumpsuckers. Local fishermen believe that seals prefer lumpsuckers to salmon. Lumpsuckers eat lobsters.

Use the information given above to construct three arguments *in favour* of action to reduce the number of seals breeding on the Farne Islands and three arguments *against* such action.

SAQ 25 (*Objective* (*c*)) Charles Darwin quoted the following figures: 100 heads of red clover produced 2 700 seeds, but the same number of heads protected from the attention of humble-bees produced not a single seed. He quoted Colonel Newman as saying 'more than two-thirds of them (i.e. humble-bees) are destroyed all over England' by field-mice, and also 'near villages and small towns I have found the nests of humble-bees more numerous than elsewhere'.

Darwin put forward the following hypothesis: '. . . the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district'.

(a) Read statements (i)–(ix), then arrange some of them in a sequence to support Darwin's hypothesis.

(b) Try to arrange some of the statements in a sequence to form a different hypothesis.

(i) Elderly ladies who keep cats choose to live in villages rather than in solitary cottages.

(ii) Farmers often have granaries infested with rats and mice.

(iii) Cats kill field-mice.

(iv) Farmers cut down trees except sometimes along field boundaries.

(v) Humble-bees nest in burrows in short grass.

(vi) Owls feed on small rodents including field-mice.

(vii) Many houses in villages have gardens with lawns and trees.

(viii) Owls wait in trees and pounce when they hear a rustle of small animals in the grass.

(ix) Farmers keep cats to control rats and mice in their buildings.

6 Summary of Unit 21

All individual organisms belong to assemblages of individuals called communities; these usually include individuals of many different species. Individuals and species are not randomly distributed; they must be able to survive under the physical, chemical and biological conditions of their environments, and barriers may prevent them from reaching suitable environments. An ecosystem consists of a community of organisms in its environment and forms a unit whose structure can be studied in terms of energy flow and the cycling of nutrients. The comparison of the River Thames and Wytham Wood shows great differences between diatoms and trees as producers and consequent differences in other trophic levels; these are relevant to problems of producing food for human beings. Study of the cycling of minerals shows why decomposers are important and why modern agriculture depends on fertilizers.

Studies of numbers of individuals show that some species are common and others rare; some species fluctuate greatly in numbers, others remain fairly stable. To attempt to explain these differences requires data that can be arranged as life tables so that mortalities for different ages can be compared. Analysis of mortalities using *k*-values reveals which are the key factors, mainly responsible for the changes in numbers from generation to generation, and which are the regulating factors that tend to stabilize the population and so are responsible for whether the species is common or rare. The tawny owl population is subject to strong regulation and is stable in numbers but the winter moth population fluctuates very considerably because the regulating factors cannot compensate fully for the key factor mortality. Understanding population dynamics helps in the planning of pest control, especially in the specification of biological control 'agents'.

Natural communities undergo succession and change with time towards a fairly stable climax. Interference may result in a deflected climax, as illustrated by the effect of rabbits, originally introduced as luxury food, on British vegetation.

Human civilization has considerable effects on other organisms, especially through agriculture and pollution. The recent rate of increase in the human population may slow down; but feeding the present and future populations requires strict application of ecological principles, the development of new sources of food and also of new sources of energy.

Objectives of Unit 21

The Objectives fall into four groups. Objective 1 covers understanding of ecological terminology. Objectives 2–6 are concerned with the organization of communities in terms of energy flow and the cycling of nutrients. The third group, Objectives 7–11, are based on the study of stability or changes in population numbers. Finally, Objectives 12–15 are related to the study of communities in their environments.

Now that you have completed this Unit, you should be able to:

1 Define and explain how biologists use the terms marked by asterisks in Table A (*SAQs 1, 3, 7, 12, 19 and 22*).

2 Interpret a given food chain or web by stating the categories of the organisms in it (*SAQ 4*).

3 Interpret a given energy flow diagram and work out assimilation, respiration and production values for the organisms in it (*SAQs 5 and 6*).

4 State the part played by different categories of organisms in the cycling of carbon, nitrogen, phosphorus and sulphur in ecosystems (*SAQ 8*).

5 Show how the principles of energy flow and mineral cycling can be related to problems of human food production (*SAQs 9, 10 and 11*).

6 Explain how agricultural ecosystems differ from natural ecosystems (*SAQ 22*).

7 Construct life tables and survivorship curves from relevant data and interpret these by stating how mortality rates vary at different ages (*SAQs 13 and 14*).

8 Calculate *K* and *k*-values for a population from relevant data (*SAQs 15 and 16*).

9 Interpret graphs with *K* and *k*-values by stating which are likely to be the key factor mortality and which the regulating mortality factors: from data, suggest hypotheses about how these mortalities actually work (e.g. by altering the food supply) (*SAQ 17*).

10 Explain the relevance of *k*-value calculations to the control of insect pests (*SAQ 18*).

11 Explain the observed changes in numbers of human populations and discuss possible future trends (*SAQ 23*).

12 Suggest, or assess, hypotheses explaining the observed distribution of species of organisms in terms of their tolerance of physico–chemical factors and their past history (*SAQ 2*).

13 Suggest, or select from a list, the types of changes in plant communities that might result from changes in environmental factors, and give reasons for your suggestions (*SAQ 20*).

14 Suggest, or select from a list, the factors that should be investigated before a given foreign species or a given chemical substance is introduced into an environment (*SAQ 21*).

15 Give examples of the impact of human activities on the environment and be prepared to argue on *ecological grounds* about the merits of proposed conservation measures (*SAQs 24 and 25*).

SAQ answers and comments

SAQ 1 (a) False—many species are included.

(b) True—contrast plants of tropical forest, desert, Arctic tundra.

(c) False—contrast plants of British chalk hills and granite.

(d) True. Some animals, for example the koala, have very narrow food preferences, so their distribution depends on the distribution of their plant food.

(e) True. The definition is correct but in practice animals move in and out, plant seeds are blown in and out and water often flows through.

SAQ 2 *Hypothesis* (*ii*) is very unlikely; it depends on an interpretation of the history of the Earth that is incorrect (as you will learn in a later Unit).

Hypothesis (*i*) is just possible but unlikely; it assumes that the same change in physiological tolerance of temperature has happened all over the world. It is much more likely that such a physiological change would happen only in a restricted region, leading to a new subspecies there.

Hypothesis (*iv*) also is just possible but very unlikely; plant seeds are often distributed by being carried on animals and it could happen with fish eggs. But the birds would have to make the flight from Europe to the tropical mountains in a short time. It is very unlikely that trout eggs would survive a flight to New Zealand, wherever they came from.

Hypothesis (*iii*) is the most plausible—and is the true explanation. Brown trout were transplanted into many parts of the world by enthusiastic sportsmen (usually British!). The original area is more likely to be northern Europe because of the wide distribution there—and this is true also. There are no native salmonid fishes in New Zealand.

So the rank order of descending plausibility is: (iii), (iv) and (i), (ii).

SAQ 3 (a) False.

(b) True, both categories depend ultimately on plants.

(c) True.

(d) False. Energy flows through an ecosystem and is dissipated as heat; there is no recycling.

(e) True in general, but some depend almost wholly on animal remains and others on plant litter.

(f) True. Annual production may be less than the mean biomass or many times greater (recall the contrast between diatoms and oak-trees).

(g) False. Usually some of it becomes litter without ever being consumed by herbivores, and some may be stored, for example as woody biomass.

SAQ 4 (a) *Herbivores* Limpets, mussels and flat periwinkles, (i), (v) and (vi); you should have recalled from the Thames study that diatoms are plants.

First carnivores Barnacles (assuming the zooplankton is herbivorous), dogwhelks (when feeding on mussels), turnstones (when feeding on limpets and periwinkles), (iv), (ii) and (viii).

Higher carnivores Dogwhelks (when feeding on barnacles), turnstones (when feeding on dogwhelks), (ii) and (viii).

Detritivores Crabs and gulls, (iii) and (vii).

Decomposers No decomposers are listed under (i)–(viii).

(b) Possible food chains are:

phytoplankton → zooplankton → barnacles → dogwhelks → turnstones

phytoplankton → mussels → dogwhelks → turnstones

mussels → (dead) → crabs—(dead) → gulls

diatoms (on seaweeds) → flat periwinkles → turnstones

diatoms (on rocks) → limpets → turnstones

So there are several different food chains present. A food web would be a better description of the system (note how dogwhelks and especially turnstones appear in more than one chain).

SAQ 5 Recollect that food assimilated A = respiration R plus production P; so the values (all $\mathrm{kJ\,m^{-2}\,y^{-1}}$) are:

U: $A = 70$ (voles)

V: $P = 26$ (grasshoppers)

W: $R = 13.8$ (sparrows)

X: $A = 15.3$ (squirrels)

Y: $P = 46$ (bleak, growing slowly because of overcrowding)

Z: $R = 624$ (African antelopes)

SAQ 6 (a) Remember that all values are $\mathrm{kJ\,m^{-2}\,y^{-1}}$.

K = net primary production = gross primary production − respiration $= 4 \times 10^4$

L = respiration = assimilation − production $= 10.3 \times 10^3$

M = production = assimilation − respiration $= 0.2 \times 10^3 = 200$

N = assimilation = respiration + production $= 100$

Q = production = assimilation − respiration $= 0.2 \times 10^4 = 2 \times 10^3$

(b) As sunlight leads to box V, this box must represent plants. Box Z has arrows to it from all the others, so this must represent detritus plus decomposers. Therefore, box W = herbivores; box X = first carnivores; box Y = higher carnivores. So the minimum values of the arrows (in $\mathrm{kJ\,m^{-2}\,y^{-1}}$) are:

arrow A = assimilation of herbivores $= 12 \times 10^3$

arrow B = assimilation of first carnivores $= 1.5 \times 10^3$

arrow C = assimilation of higher carnivores = N $= 100$

arrow D = (net primary production) − (assimilation of herbivores)
$= \mathrm{K} - \mathrm{A}$
$= (4 \times 10^4) - (12 \times 10^3)$
$= 2.8 \times 10^4$

arrow E = (production of herbivores) − (assimilation of first carnivores)
$= (1.7 \times 10^3) - (1.5 \times 10^3)$
$= 0.2 \times 10^3$
$= 200$

arrow F = (production of first carnivores) − (assimilation of higher carnivores)
= M − N
= 200 − 100
= 100

arrow G = production of higher carnivores
= 40

Remember that assimilation = consumption − faeces. As faeces form detritus the values calculated for arrows D, E and F are realistic.

(c) There are several ways of solving this problem. One way is to add up all the values of R and compare this with the gross primary production; total R is 7.966×10^4, which is less than the gross primary production (9×10^4), so there must be either net accumulation of energy or net export. There is accumulation of 2×10^3 (Q, the production of the decomposers), but there is still a net export of $8.34 \times 10^3\,\mathrm{kJ\,m^{-2}\,y^{-1}}$.

Another way is to add up the values of arrows D, E, F and G and compare the total with the consumption of decomposers: the total is 2.834×10^4, which is greater than 2×10^4; so again, there must be export (of detritus) from this ecosystem. The export value is again $8.34 \times 10^3\,\mathrm{kJ\,m^{-2}\,y^{-1}}$.

SAQ 7 (a) True. If this seems to contrast with the dissipation of food energy as heat, recall that energy is conserved but changes in form.

(b) True. This ecosystem contains all the 'ingredients' for the cycling of carbon and minerals and it has an input of energy in the form of sunlight; it should gradually warm up, and would eventually 'die' through over-heating unless some form of heat-exchanger with the outside was present.

(c) False. Mineralization is the opposite process, the breakdown by micro-organisms of organic compounds and the formation of mineral salts.

(d) False, because the food relationships are really quite different. The zooplankton are able to engulf whole tiny plants whereas the caterpillars bite small chunks off relatively enormous plants. Both sets of organisms are herbivores but their niches are very different.

SAQ 8 (i) and (v), green plants and decomposers.

Green plants absorb nitrogen (or phosphorus or sulphur) as a mineral salt from soil water or, in the case of phytoplankton, from the surrounding water; they use the salts in the synthesis of body components such as amino acids (you will study this process later).
Decomposers break down the complex organic compounds in detritus, ultimately to mineral salts; several species of decomposers may be needed for the complete break-down. The other categories are *not* essential but they speed up the mineral cycles that, in their absence, would be extremely slow. Herbivores feed on plants and produce detritus through their faeces; carnivores feed on herbivores, and the two categories of animals together, through their deaths, make the complex organic compounds synthesized by the plants available sooner to the decomposers. Detritivores speed decomposition by breaking up large pieces of detritus or dead bodies, thus providing easier access for the decomposers. Re-read Section 2.5 if you had any difficulty with this.

SAQ 9 The addition of either A or B separately leads to some increase in the rate of growth of the crop, but the effect of adding them both is much more spectacular. You can deduce that the soil is deficient in substances supplied in both A and B. Notice that the curve showing the effect of adding both fertilizers rises to a plateau and then levels out; this indicates that some other factor limits the rate of growth when A and B are both supplied in excess. This third factor could be another mineral salt or it might be the water supply or even the amount of light available.

SAQ 10 Clover is a legume with root nodules containing nitrogen-fixing bacteria, so when this crop was grown and ploughed in, there was an addition of nitrogen compared with the previous year and this promoted the growth of the wheat, a crop that requires high nitrogen for good growth. The roots and hay fed to stock during the winter resulted in the manuring of the field by the stock, so the mineral salts were conserved and made available by decomposition ready for the sowing of barley in the spring. These farmers either used the straw for their beasts and then distributed manure onto the fields and ploughed it in or ploughed in straw after the harvest. All that they removed from their land were the grain of the two cereal crops and milk, meat and other products of their stock.

SAQ 11 The two most feasible ways are to:

1 Catch the anchoveta and use these small fishes as food. They are first carnivores and eating them puts people into the category of second carnivores.

2 Dig up the guano from the islands and use it as phosphate fertilizer to promote the growth of crops in areas where the soil is deficient in phosphorus. People eating these crops would be in the category of herbivores, using the sun's energy efficiently. In the sea ecosystem, the guano birds are top carnivores but they make phosphate from the sea available for use on land.

In fact, in the past, the guano was mined and sold as fertilizer; but more recently, anchoveta have been caught in large numbers and then converted to fish meal to feed poultry, pigs and cattle *not* people. The reduction in the numbers of anchoveta led to mass mortalities of guano birds, so supplies of phosphate fertilizer have ceased to be available.

SAQ 12 (a) False. Pre-reproductive mortality must leave two survivors to replace the parents.

(b) False. They do sometimes but not always; see Figure 9b.

(c) False. They may be; but often they are catastrophic factors related to weather and totally unrelated to density.

(d) False. The meaning of specific is that the parasite species will attack only a single (or very small number of related) species of host.

(e) False. Usually some k-values vary, resulting in changes in the population.

(f) True. They kill a higher proportion of a more dense (crowded) population and a lower proportion of a less dense population and, consequently, tend to bring the numbers towards a medium value.

(g) False as a general statement. If an efficient agent is found then biological control is more efficient and much less costly than the use of chemicals; but it is not always possible to find a suitable agent.

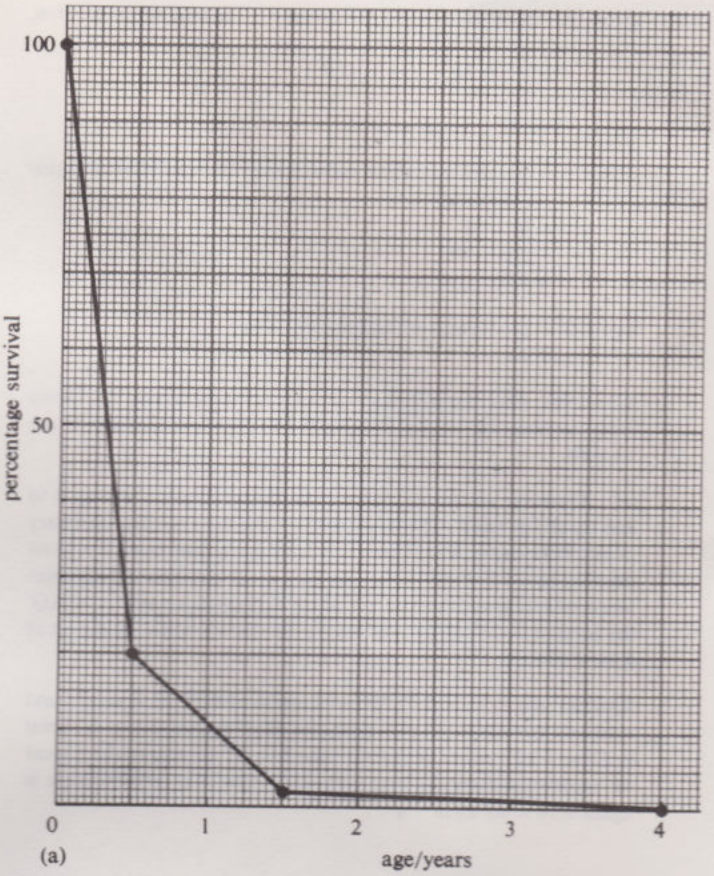
(h) False; the true definition is given in answer to (f). A mortality that kills the same number of individuals each year, irrespective of the population density is obviously 'density independent'; another type of density independent mortality is due to catastrophic factors.

SAQ 13 (a) (i) Out of 3 200 eggs, 640 survive, so 2 560 die—a mortality of 80 per cent.

(ii) Out of 640 fry, 64 survive, so 576 die—a mortality of 90 per cent.

(iii) Out of 64 smolts, 2 survive, so 62 die—a mortality of about 97 per cent.

(b) The total pre-reproductive mortality for salmon is 3 198 out of 3 200 = 99.97 per cent (see Figure 23).



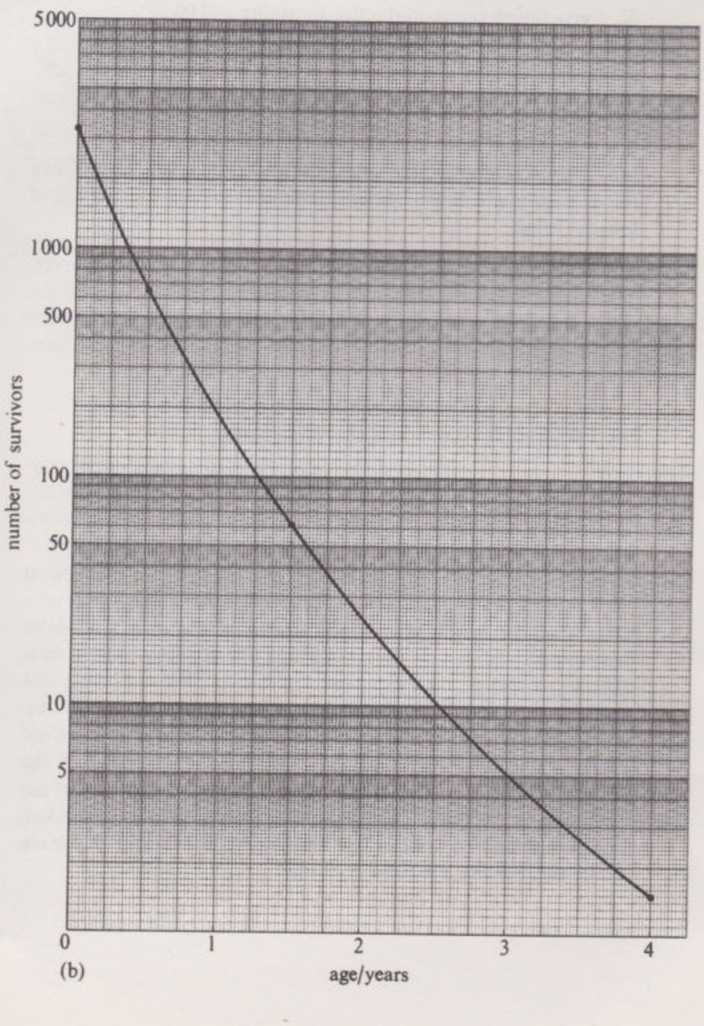


FIGURE 23 Sockeye salmon. (a) Survivorship curve on an arithmetic scale. (b) Number of survivors on a log–linear scale.

SAQ 14

	(a) Number	(b) Life table
eggs laid by female moth	200	100
caterpillars surviving the winter	16	8
caterpillars surviving *Cyzenis* attack	15	7.5
caterpillars surviving other parasites	13.5	6.75
caterpillars surviving disease	11	5.5
pupae surviving predators in the soil	2.5	1.25
pupae surviving *Cratichneumon* attack and becoming adults	2	1

SAQ 15 The calculation can be laid out thus:

	Number	*k*-values
number of eggs	200	
		$k_1 = 1.097$
number surviving 'winter disappearance'	16	
		$k_2 = 0.028$
number surviving *Cyzenis*	15	
		$k_3 = 0.046$
number surviving other parasites	13.5	
		$k_4 = 0.089$
number surviving disease	11	
		$k_5 = 0.643$
pupae surviving predators	2.5	
		$k_6 = 0.097$
number of adults	2	

K = generation pre-reproductive mortality = 2.00
= sum of *k*-values

SAQ 16 (a) The values are:

	Year							
	1966	1967	1968	1969	1970	1971	1972	1973
k_E	0.463	0.696	0.930	0.169	0.202	0.877	0.798	0.944
k_L	0.131	0.294	1.288	0.208	0.145	0.336	0.254	0.214
k_P	0.691	0.687	1.699	0.336	0.681	1.522	0.658	0.314
K	1.285	1.677	3.917	0.713	1.028	2.735	1.710	1.472

Example For 1966,

$N_E = 2\,120$

$k_E = \log 2\,120 - \log 730 = 0.463$

$N_L = 730$

$k_L = \log 730 - \log 540 = 0.131$

$N_P = 540$

$k_P = \log 540 - \log 110 = 0.691$

$N_A = 110$

$K = k_E + k_L + k_P = 1.285$

K also equals $\log 2\,120 - \log 110 = 1.285$

(b) It is not really possible to identify the key factor without drawing a graph (see SAQ 17) but k_P has the highest values and shows the greatest changes so it would be the first choice for further investigation.

SAQ 17 (a) The values of k_S vary in very much the same way as K (except for 1973), so starvation is probably the key factor mortality.

(b) Plotting k_P on Figure 22 shows that it varies in a very similar way to K, so it *is* likely to be the key factor. This implies that starvation acts by killing cinnabar moths during the pupal stage. Perhaps starved caterpillars form under-sized pupae that soon die.

(c) No. None of the *k*-values show obvious variations in the opposite direction to K. This population shows enormous swings in density suggesting that any regulating factor is very weak; the situation is much closer to that for winter moth than that for tawny owls.

SAQ 18 (a) An insect pest is a common species that attacks some product of economic value and makes it less valuable or useful.

(b) Regulating mortality factors for pest populations either do not exist or else they operate to maintain population densities that are so high that the species is common (and therefore a nuisance). Recall that this is in contrast to rare species for which the regulating mortality factors must be very effective in maintaining low population numbers.

(c) Biological control is the introduction of an 'agent' (some other species of organism) that reduces the population of the pest species and regulates it at a sufficiently low level for it not to be a nuisance.

(d) (i) A suitable 'agent' must be identified and then reared in sufficient numbers for introduction into the pest's area. The effort involves searching for suitable agents, through published information and in areas where the pest species is not a pest, and then screening such agents for possible disastrous side-effects (e.g. the possibility that they might attack some useful species). So there must be an outlay of time and effort by scientists and supporting technical staff. The outcome of the search is not fully predictable; but it is now possible to define many of the characteristics needed for a successful agent.

(ii) If an agent really is successful, then in many cases there is no need for further effort except to ensure that the agent is not affected by any other treatments applied to the resource. Under some special conditions, for example, in glasshouses, it is necessary to introduce the agent every season and to keep it in culture and breed it up at the right time.

(e) By analysing life tables and calculating *k*-values it is possible to identify the main causes of mortality and to recognize which are key factors and which are regulating factors. Comparing conditions in localities where the species is a pest and some where it is not may lead to the identification of possible biological control agents. The comparison may also show that some modification of an agricultural process may change the status of the pest by causing a high mortality; for example, disturbing the soil either earlier or later may kill some pest at a stage in its life cycle when it is in the soil.

(f) Knowledge of the population dynamics of a pest insect may allow the application of chemicals to be planned to reinforce a naturally high mortality and to avoid interference with 'helpful' organisms such as predatory insects.

(g) The use of highly 'specific' chemical agents such as pheromones or systemic insecticides or purified viruses (as dusts). All these will harm only the target species.

SAQ 19 (a) False. The climax vegetation consists of equilibrium plants. (b), (c) and (d) are all true. During a succession, the community becomes more diverse and the environment is modified, so the biotic factors become more complex and the physico-chemical environmental factors become less stringent.

SAQ 20 In the first year after the catastrophe, pioneer plants should colonize the area. These will be lichens and mosses on the rocks, and there may be small herbs (flowering plants) forming mats over the sand and gravel. Over the following 50 years, there should be a succession of plant species, each group changing the environment and making it more suitable for the next stage in the succession. The pioneer plants should be replaced by opportunists, mainly annuals producing large numbers of wind-blown seeds, and gradually more and more species should establish themselves. The equilibrium species in Britain are likely to be those of some type of

woodland. In the climax community there will be trees, shrubs, and herbs. During the succession, the tendency should be for the vegetation to become taller and more dense and for the communities to become more complex, with many more species. The harsh environment of bare rock, gravel and sand is transformed by the accumulation of litter and soil development into a place where many plant species can live, if they can establish themselves in the face of competition from other species.

SAQ 21 You would wish to evaluate the possible effects of introducing the new species into British plant and animal communities. The foreign species could affect native species (cultivated and wild) by competing for a food supply or for living space or (if herbivores or predators) by consuming native species and so altering food webs. There is also the danger of introducing, together with the foreign species, organisms that could become pests or lead to diseases and have devastating effects on native species. This danger could be mitigated by quarantining the foreign species—cultivating it under isolation to clear it of pests and diseases as far as possible. To take the three examples:

(a) *Reindeer* are herbivores with a limited food preference—they would not compete with native sheep or cattle or native deer. Their activity might lead to soil erosion through the eating out of lichens—the probability of this could be judged by comparing the environment in Scandinavia with that in Scotland. It is unlikely that native predators would be able to tackle such large animals. Reindeer are now herded near Aviemore in Scotland.

(b) *Canadian pondweed* was introduced into Britain in 1842; it propagated itself so vigorously that it soon choked drainage ditches in the Fens and also some rivers and canals. After flourishing at a nuisance level between 1850 and 1880, it began to propagate less luxuriantly (the cause for this is not understood). Now it is a very common plant and is considered useful because it adds much oxygen to the water and supports many animals that are valuable food for fishes. An experimental introduction under conditions in which the plant could not spread to other waters might have revealed its undesirable (in the short term) vigour but not its long-term usefulness.

(c) The colourful *Colorado beetle* is a pest in the USA and in Europe. A very brief investigation of the devastation it causes to potato fields in both continents would be sufficient to convince any reasonable person that it should be kept out of the British Isles. In fact, there are regulations forbidding its introduction here. Small numbers of live beetles have occasionally been found in southern counties in summer; immediate efforts to eradicate them before the species could become established have so far been successful. The bright colours are associated with unpalatability to insectivorous birds so the beetle has no predators.

SAQ 22 (a) True.

(b) False. Weeds are a sort of opportunist plant.

(c) False. Most pests are probably herbivores, feeding either on growing plants or on stored products of vegetable origin.

(d) True.

(e) False. Recall from Section 3.3 that these have given rise to many problems and that biological control or some form of integrated control is more acceptable.

SAQ 23 All three countries have about one-third of the population between 15 and 39 years old, in the age group when women have babies. In Canada, the rest of the population is equally divided between those younger and those older than the 15–39 age group, but France has more than 40 per cent older than 39 and Iran has more than 40 per cent younger than 15. If France is typical of Western Europe, the birth and death rates are both low whereas in Canada the birth rate is probably higher (in the region of 3 per cent) and the death rate is low. Iran probably has a high birth rate and has had, until recently, a high death rate; it is probably now like Northern Africa in Table 9. A demographer would probably expect France to continue to have almost zero growth in population, with an increase in the proportion of older people. In Canada, the population is likely to continue to grow as the young people begin to marry and have children; but the birth rate should decrease and Canada should become like France by the end of the century. Iran is probably faced with a population 'explosion' as its young people grow up and have children; with better medical aid, a high proportion of babies will survive and the present adults are all likely to live longer. Demographers would expect Iran eventually to show a drop in birth rate. These population projections assume there will be no disasters, such as wars or epidemics with very high mortalities; they also assume that demographers are right to believe that birth rates eventually fall as countries become more developed.

SAQ 24 Possible arguments in favour of reducing the number of seals that breed on the Farne Islands are:

1 Seals eat salmon, cod and plaice, all valuable fishes (they also damage salmon nets by taking fish out of them)—and thus reduce our potential food supply.

2 The number of seals has increased so markedly since the 1930s that it appears that any natural balance has been upset and the numbers may just go on increasing indefinitely.

3 Where there are many seals, there is a higher mortality of calves; to allow the total number of seals to go on increasing will lead to greater suffering among calves; to reduce the number of seals will reduce suffering.

Possible arguments against reducing the number of seals that breed on the Farne Islands are:

1 The grey seal is a rare species; 75 per cent of the world population lives in British waters; we have a responsibility to protect them and it would be wrong to kill any.

2 Reducing the number of seals will mean more lumpsuckers and hence fewer lobsters; lobsters are a prized delicacy that should be protected.

3 As the proportion of calves dying is higher where the seals are more crowded, reducing the number of breeding seals may not in fact reduce the number of adults because the total number of calves surviving may be the same as at present. This death of calves may be the regulating factor and interference with this may lead to unexpected results.

SAQ 25 Darwin assumed that the number of field-mice determines the number of bees and that clover plants will grow only where bees have visited the flowers. If there are more bees near villages and small towns, this implies that there are fewer field-mice there. Darwin suggested that the low numbers of field-mice are the result of the presence of many cats near villages and small towns.

Of the nine statements, (v) followed by (vii) account for the presence of humble-bees near villages; (iii) followed by (i) account for the absence of field-mice near villages; (ix) implies that there could be many cats in the countryside but (ii) explains that these cats probably hunt in granaries and do not molest the field-mice that eat the humble-bees.

(a) So Darwin's hypothesis is supported by the observations in statements (v), (vii), (iii), (i), (ix) and (ii).

(b) An alternative hypothesis is supported by statements (v), (vii), (vi), (viii), (iv) and (vii) again. It is that the number of field-mice is controlled by owls; these birds hunt from trees; there are few suitable trees in the countryside because farmers cut them down, but there are suitable trees in village gardens; hence there are fewer field-mice near villages and therefore (from Colonel Newman's statements) more humble-bees and so probably more clover (from Darwin's own statement).

List of Filmstrips for Unit 21

Filmstrip 21.1,	Frame 1	Bracken *Pteridium aquilinum*, a fern that is common in Britain and widely distributed through the world.
	Frame 2	Common reed *Phragmites communis*, a grass that grows in water and damp places and is common through the world.
	Frame 3	Flowering head of common reed *Phragmites communis*.
	Frame 4	Part of an oak-wood that has recently been cleared; the large trees are oaks *Quercus robur* and the shrubs are hazel *Corylus avellana* with a dense growth of herbs below them.
	Frame 5	Mixed oak–sycamore woodland with clearings and thick undergrowth. The nearest trees are sycamore *Acer campestre*; the large tree in the middle distance is an oak *Quercus robur*.
	Frame 6	Roach *Rutilus rutilus* in an aquarium.
	Frame 7	Tawny owl *Strix aluco* (in a zoo).
Filmstrip 21.2,	Frame 8a	Winter moth *Operophtera brumata* female climbing up an oak trunk in November.
	Frame 8b	Winter moth *Operophtera brumata* male copulating with a female on an oak trunk.
	Frame 9	Winter moth *Operophtera brumata* caterpillar.
	Frame 10	Cottony cushion scale *Icerya purchasi* on a citrus stem.
	Frame 11	Lullington Heath, Sussex, on 23 March 1954.
	Frame 12	Lullington Heath, Sussex, on 21 February 1967.
	Frame 13	Old Winchester Hill, Hampshire, on 10 August 1954.
	Frame 14	Old Winchester Hill, Hampshire, on 13 August 1956.
Filmstrip 21.3,	Frame 15	View of Chiltern Hills (Aston Rowant) with Nature Reserve and Motorway (M40).
	Frame 16	Aerial view of part of Aston Rowant Nature Reserve showing the fence to keep out rabbits, small ungrazed plots and meadow heavily grazed by sheep.
	Frame 17	Rockrose *Helianthemum chamaecistus* plants grazed by rabbits.
	Frame 18	Rabbit warren showing patches of stinging nettles *Urtica dioica*.
	Frame 19	Ant-hill in a lightly grazed meadow in summer.
	Frame 20	Area with ragwort plants *Senecio jacobaea* in summer.
	Frame 21	Ungrazed area with scrub growing up in summer.
Filmstrip 21.4,	Frame 22	Clustered bellflower *Campanula glomerata* flowers.
	Frame 23	Rockrose *Helianthemum chamaecistus* flower.
	Frame 24	Majoram *Origanum vulgare* in flower.
	Frame 25	Scabious *Scabiosa columbaria* flower.
	Frame 26	Pyramid orchid *Anacamptis pyramidalis* flowers.
	Frame 27	Greater knapweed *Centaurea scabiosa* flower with a hoverfly (order Diptera, family Syrphidae).
	Frame 28	Wild carrot *Daucus carota* in flower with a burnet moth *Zygaena filipendulae* (order Lepidoptera).

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